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THE UNIVERSITY OF ALBERTA

AN ECOPHYSIOLOGICAL STUDY OF THE EFFECTS OF THERMAL DISCHARGES ON THE SUBMERGED MACROPHYTES OF LAKE WABAMUN

by

© E.DALE ALLEN

A THESIS

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EDMONTON, ALBERTA

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "An Ecophysiological Study of the Effects of Thermal Discharges on the Submerged Macrophytes of Lake Wabamun" submitted by E. Dale Allen in partial fulfilment of the requirements for the degree of Master of Science in Ecophysiology.

Supervisor

August 20, 1973.

ABSTRACT

A combined field and laboratory study was carried out to determine the effects of thermal discharges from two power generating stations on the submerged macrophytes of Lake Wabamun, Alberta.

The distribution of submerged macrophytes in Lake Wabamun was mapped and other lakes, mostly in central Alberta, were explored starting in 1970. Lake Wabamun was found to be unique in having a heavy growth of *Elodea canadensis*, which is otherwise rare in the area. Heavy growths were found in zones influenced by the heated discharge from the older 600Mw power station. A search of earlier records indicated that *Elodea* had not been listed for the lake before 1968. It was concluded that the *Elodea* community had appeared in the lake within the preceding 10 years. The second, 300Mw station began operation in late 1970. *Chara* was soon killed in an area around the mouth of the discharge canal and was immediately replaced by *Elodea*. Between 1971 and 1973 the 3 acres occupied by *Elodea* expanded to 90 acres. The distribution of *Elodea* roughly coincides with the zones most affected by the heated discharges from the power stations.

Light measurements in open water and under ice were made with a waterproofed spectroradiometer and a quantum meter (400 - 700nm) to determine the quality and intensity in the photic zone. It was found that light levels in the water column varied widely with ice thickness and, particularly, snow depth. Maximum light transmission by the water occurred at 560nm (yellow-green).

Plant phenology at four sites was monitored. *Elodea* was found to mature earlier than the endemic species in the heated areas, due mainly to its ability to overwinter as growing plants of substantial

size. Mature *Elodea* commonly detaches from the bottom to form floating rafts which constitute a nuisance. Vegetative propagules are produced in larger numbers and over longer periods of time by *Elodea* than by the other species, thus enabling it to spread rapidly.

Net assimilation rates of freshly collected *Elodea canadensis*, *Myriophyllum exalbescens*, *Potamogeton pectinatus* and *Chara globularis* were measured under differing conditions of temperature light and pH in specially designed cuvettes using an oxygen electrode.

Elodea and *Myriophyllum* had the highest net assimilation - reaching a light-saturated rate of about 30mg O_2/hr/gm organic matter at 25°C. *P. pectinatus* and *Chara* reached only 16 and 6mg O_2/hr/gm organic matter, respectively. *Elodea* and *P. pectinatus* proved to be the most efficient plants at low light levels. All species were affected by pH. At pH 9 and low light intensity, *Myriophyllum* and *P. pectinatus* assimilated at 70% of their optimum rate, while *Elodea* and *Chara* assimilated at only 20% and less than 10% of maximum, respectively. *Elodea's* relatively high efficiency at low light levels agrees well with its ability to grow at greater depth than the other species. The inability of *Chara* and, to a lesser extent, *Elodea* to assimilate efficiently under conditions of high pH may partially explain their limited distribution in lakes which are naturally alkaline or become highly alkaline during algal blooms.

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Underwater light quality measurements were made possible through the use of a waterproof spectroradiometer made available to us by Dr. R.G. Wetzel of the University of Michigan.

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With them the seed of Wisdom did I
sow,
And with mine own hand wrought to
make it grow;
And this was all the Harvest that I
reap'd -
"I came like Water, and like Wind I
go."

Omar Khayyám

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INTRODUCTION

> "The vital activity of plants is, like that of animals, the result of the co-operation of two factors; the internal structure, or inherited disposition, and the influences operating from without, or stimuli" - Julius von Sachs, Lectures on the Physiology of Plants. 1882

That plants react to their environment is well known from observations made of their distribution and behavior in nature. Each plant has its own particular set of physiological requirements which determine where, and under what conditions it will be successful. The method of growth, of propagation or resistance to temporary adverse conditions may enable a plant to gain advantage over its competitors.

This study began in 1970 with a survey of the submerged aquatic macrophyte communities in Lake Wabamun, Alberta. The survey was initiated in response to public complaint over unusually heavy growths in Kapasawin Bay that were being blamed on the discharge of heated water by a 600-megawatt (Mw) power station whose first 75 Mw unit was commissioned in 1956.

As a result of this survey, and a survey of other lakes in central Alberta which followed, it was found that the receiving waters of Kapasiwin Bay supported heavy growths of *Elodea canadensis* Michx., a species found only rarely and in small quantities in other bodies of water in the area.

A number of reports (unpublished) written in the early 1960's and an extensive report by Stanley and Dobson (1961) on the aquatic plants and the thermal effluents in Lake Wabamun did not mention the presence of *Elodea* in the lake. The principal species listed in Kapasiwin Bay were *Myriophyllum exalbescens*, *Chara* sp. and *Potamogeton zosteriformis*. *Elodea* was noted for the first time in Lake Wabamun by Wheelock (1969)

in 1968. He reported it in the heated effluent in Kapasiwin Bay and included a photograph of a dense patch in a flowering condition. It appeared that at some time between 1964 and 1968 an invasion of Kapasiwin Bay had occurred in which the original species were displaced to a great degree by *Elodea*.

During the winter of 1970 a second power station (300 Mw) was commissioned at Sundance on the opposite side of the lake. In September of 1971, *Elodea* began to invade an area located a short distance out from the mouth of the Sundance discharge canal where *Myriophyllum* and *Chara* had previously been growing. Allen and Gorham (1973) have suggested that a combination of low light and elevated temperatures caused *Chara* to die and be replaced by *Elodea*.

It became of interest therefore, to know precisely how *Elodea* gained such an advantage over the established species, especially in the waters receiving the heated effluents from the discharge canals of the power stations. This study was undertaken to examine two likely possibilities in some detail using a combination of extensive field observations and laboratory experimentation. One possibility was that year-round ice-free conditions led to the growth and development of *Elodea* at the expense of the original species because of differences in winter dormancy. The other possibility was that the heated effluent directly promoted higher net assimilation, hence more growth of *Elodea*, than of the original species.

Four of the major species in Lake Wabamun were chosen for study: *Elodea canadensis* Michx., *Myriophyllum exalbescens* Fern., *Potamogeton pectinatus* L. and *Chara globularis* Thuill. Field observations were made throughout the entire year for a period of three years to determine

their phenologies.

Net assimilation measurements were carried out in the laboratory using fresh plants collected from the lake. These were then subjected to a range of light intensities, temperatures and pH values that included those levels that were found to occur in the lake.

The field observations and laboratory experiments are described separately in Parts I and II, followed by a General Discussion in which the major conclusions from both parts are synthesized.

LITERATURE REVIEW

A considerable body of literature dealing with aquatic plants exists. Much of the earlier work was brought together by Arber (1920) in a work which is still of great relevence in the field. A comprehensive review by Sculthorpe (1967) covers nearly all the literature dealing with the anatomy, physiology, ecology and distribution of aquatic plants. The literature reviewed below is a selection of those publications which have been the most pertinent to the topics in this thesis.

Nuisance growth of introduced aquatic macrophytes.

Within the last 150 years, several species of aquatic plants have been introduced and have undergone extensive spread into new areas where they were not endemic, and because of heavy growth, they have choked lakes and rivers. The spread of the water hyacinth, *Eichornia crassipes*, in the tropics and southern United States is described in Sculthorpe (1967) as well as the spread of *Azolla filiculoides* in Europe. Arber (1920) and Sculthorpe (1967) trace in considerable detail the introduction and spread of *Elodea canadensis* in the United Kingdom in the nineteenth century. In all these cases the offending species were introduced to new areas by man, and all too often by botanists and plant enthusiasts who failed to anticipate the consequences of their actions.

Measurement of growth and productivity.

The measurement of the productivity of an aquatic plant community has been approached in several ways. Forsberg (1960) measured the standing crops by collecting the plants from a fixed area and determining their dry weight and the organic weight by difference after ashing. He also measured the fresh volume of the plants by the displace-

ment of water. An evaluation of the different weight methods is given by Westlake (1963, 1969) as well as a method for the determination of fresh weight (Westlake, 1965).

Production may be measured over shorter time periods by determining the rate of net assimilation. This may be done by measuring the rate of carbon uptake or oxygen production. Wetzel (1965) evaluated the two techniques and felt that the oxygen method had too many problems to be of general use. He cites the problems of oxygen retention in the aerenchyma and the rate of diffusion into the surrounding solution as sources of large errors. Hartman and Brown (1967) measured the volume and composition of the gas stored in the aerenchyma and found that oxygen tended to appear faster in the internal atmosphere of the plant than in the water surrounding the plant. The errors of the oxygen technique not withstanding, it remains in use - especially for physiological work rather than for field applications, e.g. Ikusima (1965), Steemann Nielsen (1947, 1952).

Wetzel (1965) advocated the ^{14}C technique for the measurement of net assimilation and described apparatus and procedures for its use.

Effects of light and temperature.

Comparatively few studies on the effects of light and temperature have been carried out especially under field conditions.

The laboratory study of assimilation by aquatic plants under a variety of conditions by Blackman and Smith (1911) remains a classic in the field. Net assimilation was determined by measuring the uptake of CO_2 from solution in an ingenious apparatus in which the amount of carbon dioxide, light and temperature could be varied.

Anderson (1969) measured the respiration of *Potamogeton perfoliatus*

which had been growing in heated water at 30 to 35°C and in unheated water at 25 to 28°C and found that the respiration rates of warm water plants were higher than those from cold water when measured at the same temperature. The lethal temperature for *P. perfoliatus* was 45°C. Wood and Zieman (1969) examined the appearance of *Thalassia* along a transect extending down stream from a power station discharging heated water into an estuarine river. The temperatures near the discharge were high enough to be lethal to the alga. Meyer and Anderson (1939) measured the rate of oxygen production by *Elodea canadensis* at several temperatures. Oxygen production remained constant at 25°C but dropped slightly after 30 minutes exposure to 30°C. At 40°C oxygen production dropped markedly after only 10 minutes. This was attributed to increased rates of respiration.

Blackburn et al. (1961) studied the effect of light on the growth of *Elodea densa* and *Heteranthera dubia*. *Elodea* was found to grow best at low light levels (about 10 foot-candles) when using daylight fluorescent lamps. High intensities caused bleaching and death. *Heteranthera* grew best at 590 foot-candles.

Meyer et al. (1943) investigated the rate of apparent photosynthesis of *Potamogeton richardsonii, Najas flexilis, Elodea canadensis, Vallisneria americana* and *Heteranthera dubia* at different depths in Lake Erie by lowering bottles containing the plants to different depths, then measuring the amount of oxygen produced after 30 minutes. The temperature of the water column was 21-22°C. *Vallisneria* was the most efficient plant, compensating at a light level less than 0.5% of the surface light level. The others compensated at less than 2% of the surface intensity with the exception of *Najas* which compensated at

a level between 2 and 3%.

Chapman (1971) describes the distribution of macrophytes in a New Zealand lake in which the exotics, *Lagarosiphon major* and *Elodea canadensis* had invaded and become established some time earlier. It was found that of the several macrophytes present including *Potamogeton* spp., *Drepanocladus*, and *Lagarosiphon*, *Elodea* was able to colonize to the greatest depths (8 m). This was possibly influenced to some degree by the fineness of the bottom sediments which were preferred by *Elodea*.

Measurement of light in water.

An extensive review of the treatment of light measurements in water is given in Hutchinson (1957) and Vollenweider (1969). Instrumentation and methods of light measurement is given in Sauberer (1962). Extensive light measurements in all planes at different depths with a collimated detector were made by Tyler (1960). Most of these studies have been made using selenium cells often equipped with a series of filters which transmit relatively wide wavebands. Comparatively few light measurements have been made of monochromatic light. Spence (1971) cites a number of references in connection with his study in which he used a spectroradiometer equipped with a fiber-optic probe to measure spectral intensity at depths down to one meter.

Units in which light levels have been expressed vary considerably and most do not have a plant physiological basis e.g. foot-candle or lux. They are of use only as relative measurements and they do not enable comparison to be made when other types of light sources are used. Spence (1971) points out that photosynthesis is a quantum reaction so that light expressed as quanta of a known energy is more

relevent to photosynthetic work. He expressed the amount of light reaching a given depth in quanta/cm^2/second as derived from the measurement of the energy of a known waveband divided by the energy per quantum at the average wavelength of the waveband being measured. The number of quanta received can be divided by Avogadro's number to give "moles" of quanta (6.01×10^{23} quanta = 1 Einstein). A treatment of these units and their derivations is given in Nobel (1970).

Carbon Sources.

The uptake of carbon by aquatic plants is quite distinct from that of land plants. In solution, carbon can occur in three forms; free carbon dioxide, bicarbonate, or carbonate ions. The relative proportions of these molecular or ionic species is determined by the pH of the solution. (See Appendix III).

Arens (1936) showed that bicarbonate ions could be used by some aquatic plants, however, it was Steemann Nielsen (1947) who investigated the effects of various concentrations of free carbon dioxide and bicarbonate on the rate of photosynthesis of several aquatic plants. He found that,with the exception of *Fontinalis antipyretica*, the plants used in the experiments could use both free carbon dioxide and bicarbonate but that the rate of bicarbonate uptake was only about 50% of the rate of free carbon dioxide uptake when the concentrations and light levels were the same.

The assimilation of carbon dioxide was independent of other ions in the solution but the uptake of bicarbonate could be enhanced by a mixture of cations such as potassium, calcium and magnesium. Significantly, he found that at a high light level of 37,000 lux, the net assimilation rate of *Myriophyllum* is independent of pH over a range of 8 to 10.2

with a bicarbonate solution of 1.5 meq/liter. Similarly from pH 5.2 to 3, the rate of assimilation was constant. At these low pH values, free carbon dioxide is the dominant form.

Bicarbonate could be reduced to quite low levels by *Myriophyllum*. At 37,000 lux an initial solution containing 5 to 10 meq/liter of bicarbonate could be reduced to less than 50% of its original carbon content. In doing this the pH rose to 11. At this pH a solution of carbonate-bicarbonate still consists of about 20% bicarbonate. Steeman Nielsen found that bicarbonate was absorbed by both sides of the leaf but hydroxyl ions were released from only the adaxial surface.

Steeman Nielsen (1951) proposed that bicarbonate uptake was linked to the uptake of cations and that the rate of uptake was limited by the excretion of hydroxyl ions from the upper surface of the leaf. Further work by Helder and Boerma (1972) with the transport of labelled rubidium through the leaf of *Potamogeton lucens* confirmed that rubidium was taken up at the lower surface of the leaf and released at the upper surface with little retention in the leaf. The polar transport of rubidium was found to be dependent upon light and bicarbonate. The direction of transport remained the same when only the lower surface of the leaf was illuminated. Helder and Boerma propose that the assimilation of bicarbonate is the only active process. They suggested that the lower leaf cells are more permeable to bicarbonate than the upper cells, while the upper cells are more permeable to hydroxyl ions. During assimilation a concentration gradient is produced across the leaf. As bicarbonate is taken up on the abaxial side, it is accompanied by a corresponding flow of cations which are excreted from the adaxial side along with the hydroxyl ions.

Steeman Nielsen (1952) found that changing light levels affected the rate of oxygen production. After going from a low light level (3,000 lux) to a higher level (100,000 lux) then returning to the original level, the rate of oxygen production during the second 3,000-lux exposure was considerably lower than the first and was often below the light compensation point. The rate recovered after some time when the plant was kept either in the dark or in light of moderate intensity. He attributed this effect to photo-oxidation, but did not measure dark respiration.

PART I

FIELD OBSERVATIONS

1970 SURVEY OF SUBMERGED MACROPHYTES IN LAKE WABAMUN

A comprehensive survey of the distribution of submerged macrophytes in Lake Wabamun was carried out in the summer of 1970 and additional observations have been made primarily in the east end in subsequent years. The survey was accomplished by the use of a plant grappel and SCUBA diving along transects which usually ran perpendicular to the shoreline. Locations were determined with a Wild Optical Rangefinder for distances up to 1,000 feet and a Hughes Class A sextant for greater distances or isolated stations. Depths were measured with a lead line or a depth gauge worn by the diver.

The results of the survey are shown in Fig. 1 and a list of the submerged and floating-leaved species is given in Table 1.

Several community types were found to occur in the Lake. One, described as mixed, consists of *Myriophyllum*, *Potamogeton vaginatus* Turcz. and *Potamogeton richardsonii* (Benn.) Rydb. with lesser amounts of *Ceratophyllum* and other Potamogetons. *Chara* forms an understory with a high degree of bottom cover. This community occurs throughout most of Moonlight Bay and near the shore of the north side of Kapasiwin Bay, west to the discharge canal of the Wabamun station. It also occurs along the west shore of Goosequill Bay.

The community which occupied most of the eastern end of the lake was almost pure *Elodea*. *Myriophyllum* occurred sparsely within it. No *Chara* grew beneath the *Elodea*. *Elodea* grew to a depth of about 4.5 m.

Chara meadows occurred in areas where the bottom is firm such as at Point Alison, the east shore of Kapasiwin Bay and east of the mixed community in Goosequill Bay. The centre of Goosequill Bay was populated very sparsely by *P. vaginatus*.

Macrophytes occurred all around the lake as localized colonies - mainly Potamogetons, some *Ceratophyllum* and *Myriophyllum*. *Chara* occurred nearly everywhere while *Elodea* was not seen west of Riche's Point.

FIGURE 1. Distribution of the submerged macrophytes in Lake Wabamun in 1970.

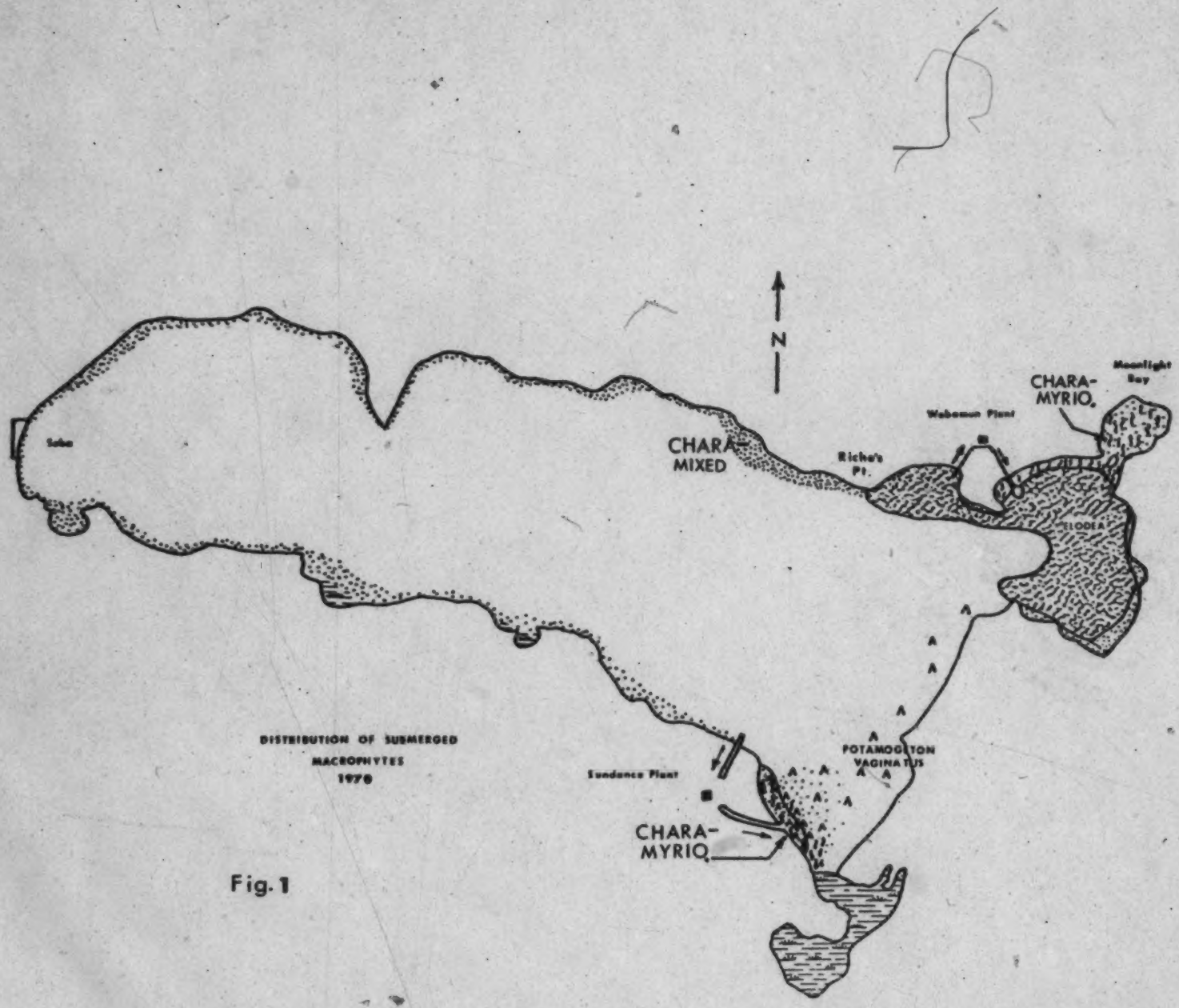

N
CHARA-
MYRIO.
Moonlight
Bay
Wabamun Plant
CHARA-
MIXED
Richo's
Pt.
ELODEA
POTAMOGETON
VAGINATUS
Sundance Plant
CHARA-
MYRIO.
DISTRIBUTION OF SUBMERGED
MACROPHYTES
1978

Fig. 1

TABLE I

Species List of Plants found in Lake Wabamun

Submerged or floating-leaved

Ceratophyllum demersum L.
Chara globularis Thuill
Drepanocladus sp.
Elodea canadensis Michx.
Hippuris vulgaris L.
Lemna minor L.
Lemna trisulca L.
Myriophyllum exalbescens Fern.
Najas flexilis (Willd) Kostk and Schmidt
Nuphar variegatum Engelm.
Polygonum amphibium L.
Potamogeton filiformis Pers.
Potamogeton friesii Rupr.
Potamogeton natans L.
Potamogeton pectinatus L.
Potamogeton praelongus Wulf.*
Potamogeton pusillus L.*
Potamogeton richardsonii (Benn) Rydb.
Potamogeton strictifolius Benn.*
Potamogeton vaginatus Turcz.
Potamogeton zosteriformis Fern.
Ranunculus aquatilis L.
Sagittaria cuneata Sheld.
Spirodela polyrhiza (L.) Schleiden
Utricularia vulgaris L.
Zannichellia palustris L.

Emergent species

Acorus calamus L.*
Equisetum fluviatile L.
Phragmites communis Trin.
Scirpus spp.
Sium suave Walt.
Sparganium leurycarpum Engelm.
Typha latifolia L.

* J.R. Allan, personal communication

OCCURRENCE OF *ELODEA* IN CENTRAL ALBERTA

Extensive collection of aquatic plants in Alberta have not been made and little is known of the geographic distribution of species or of their relations to water quality and sediment types. Some 25 lakes, mostly in central Alberta, were explored as time permitted. *Elodea*, in particular, was sought after (Appendix I). Moss (1959) listed *Elodea canadensis* but indicated that only a few records of its occurrence existed.

Most endemic species of submerged macrophytes were found in all lakes examined. Only in those which were highly alkaline was the species list noticeably reduced. The species that were much less widely distributed were *Elodea* and *Chara*.

Elodea was found in several spots in the Sturgeon River system and its associated lakes. One plant was found in Lake Isle. A small patch was found in Matchayaw (Devil's) Lake and a third patch was found in the Sturgeon River near Gibbons. *Elodea* has also been found in a small isolated pond beside Highway 16 west of Stoney Plain, locally called Danard Lake. The occurrence of *Elodea* in Alberta is summarized in Appendix II.

DESCRIPTION OF LAKE WABAMUN

Morphometry and Power Development

Lake Wabamun is located in central Alberta 45 miles West of Edmonton. The lake morphometry has been described according to the recommendations of Hutchinson (1957) by Nursall and Gallup (1971):

Elevation	722.7m
Area	82.5km^2
Volume	0.455km^3
Length	19.2km
Maximum breadth	6.6km
Mean breadth	4.3km
Maximum depth	11.6m
Mean depth	5.4m
Shoreline length	57.3km
Shoreline development factor	1.83
Area of surface drainage	372.4km^2

The hydrographic survey of Lake Wabamun is illustrated in Fig. 2.

Extensive coal deposits lying both to the north and to the south of the lake which are being strip-mined have made the location very suitable for the establishment of coal-fired electrical generating stations. The first of these, located at Wabamun, was commissioned in 1956. It initially produced 75 Megawatts, but this was increased by stages to a total of 600 Mw in March, 1968.

A second station was built on the south side of the lake at Sundance and its first unit, rated at 300 Mw, was commissioned in the fall of 1970. Both stations use water from the lake for cooling

FIGURE 2. Hydrographic map of Lake Wabamun redrawn from Government of Alberta, Department of Water Resources, 1960.

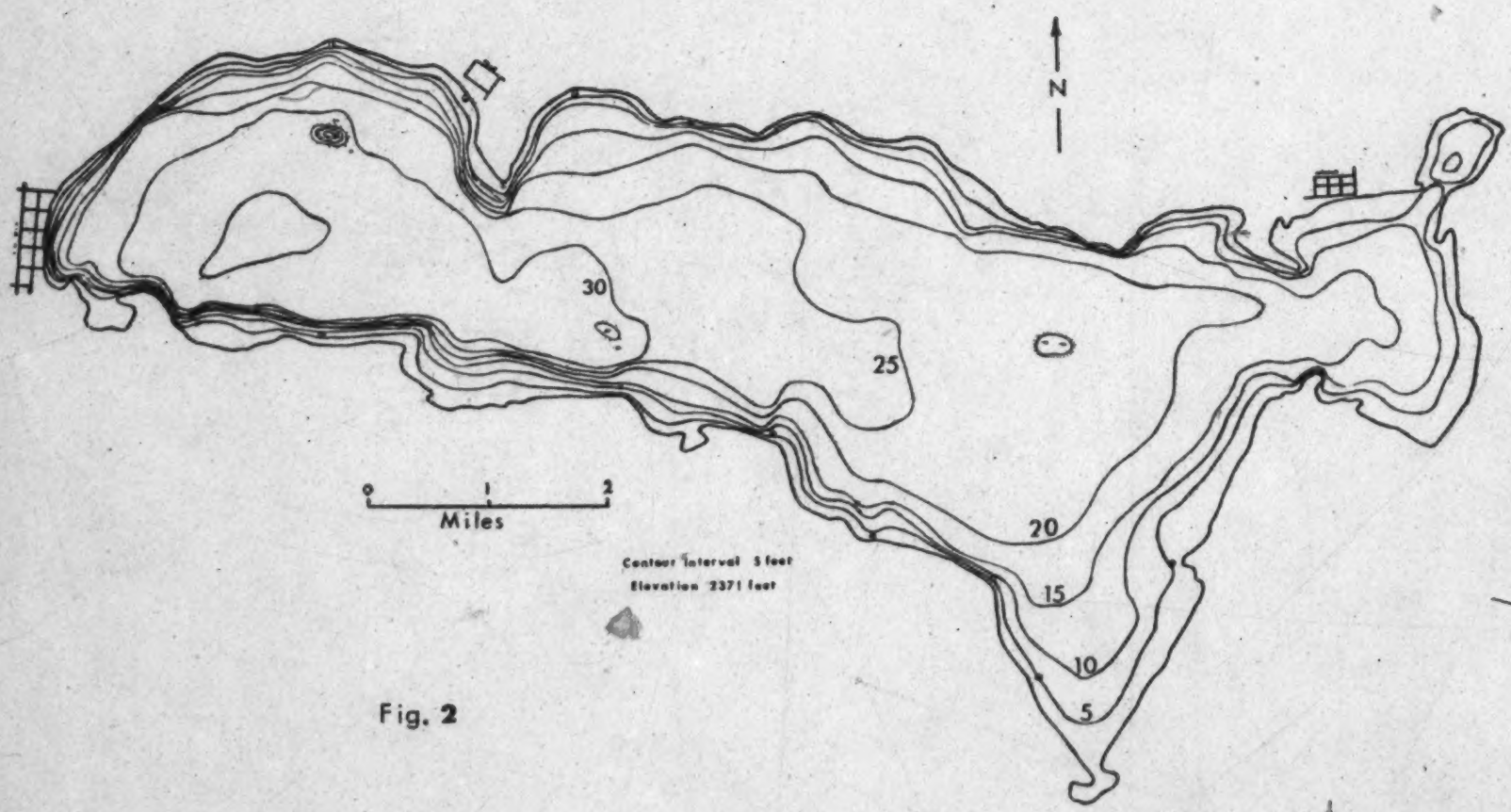

N
30
25
20
15
10
5
0
1
2
Miles
Contour Interval 5 feet
Elevation 2371 feet

Fig. 2

purposes by pumping it through canals and discharging the heated water back into the lake. The amount of cooling water used by the stations varies seasonally, the Wabamun station circulates 270,000 gallons per minute in summer and 137,000 gallons per minute in winter, while the Sundance station, with only half the generating capacity, circulates 150,000 gallons per minute in summer and 73,000 gallons per minute in winter. The stations discharge enough heat at these flow rates to raise the temperature of the cooling water about 10.5°C in summer and 14.5°C in winter (Allen and Gorham, 1972). This heat represents about 65% of the energy produced by burning the coal.

The heated effluents cause localized temperature stratifications whose intensity, depth and extent are determined by local weather conditions. In winter, the heat keeps extensive areas of the lake ice-free. The sizes of these areas vary with the air temperature and their shapes are moulded by the prevailing wind. The ice-free area at Wabamun averages about 250 hectares (620 acres) while at Sundance it is 60 hectares (150 acres). Nearly all of the lake bottom within these ice-free areas is within the photic zone (less than 4.5 m).

Water Chemistry

An extensive program of water sampling in Lake Wabamun has been carried out by colleagues with the analyses being performed in the Department of Zoology.

Wind action during the summer mixes the lake so that samples collected from various areas and depths show little difference. The water is low in orthophosphate when compared with other lakes in the area. No seasonal cycling of phosphate levels has been detected. In Table 2, the Wabamun analyses are compared with samples from

TABLE 2

Water analyses for Lake Wabamun and four other lakes in central Alberta
(All samples passed through a 0.45μ Millipore filter)

	Wabamun		Isle[1]	Wizard[1]	Banard[1]	Pigeon[1]
	Range	Mean				
pH	8.4 - 9.4	8.6	9	8.3	8-10.5	8.2
Orthophosphate, ppm	0.002- 0.03	0.01	0.41	0.04	0.5	0.01
Nitrate, ppm	0.02 - 0.05	0.03	0.05	0.11	0.05	0.02
Silica, ppm	1.5 - 8.4	2.5	5.8	2.0	0.5	3
Iron, ppm	0.02 - 0.12	0.05	0.15	0.4	0.2	0.22
Sulphate, ppm	18 - 40	26	15	9	3	8
Chloride, ppm	0.11 - 12	2.3	0.46	3.4	10	---
Total alkalinity, as $CaCO_3$, ppm	124 -180	150	141	---	50	132
Specific conductivity, μmho/cm	---	390	200	---	140	260

[1]The analyses for these lakes are for single samples collected in the summer months.

nearby Lake Isle, a very productive lake comparable in size to Wabamun which regularly produces heavy growths of submerged macrophytes and of *Aphanizomenon flos-aquae* (L.) Ralfs.; with Wizard Lake which produces macrophytes and heavy blooms of *Aphanizomenon*; Danard Lake, which contains *Elodea* and also has heavy growth of *Aphanizomenon*, and large Pigeon Lake which does not bloom and has a much lower production of macrophytes.

Sediments

The lake bottom consists generally of a fine flocculent ooze of a light brown colour which is considerably more than two meters deep in most areas. Sediment samples were taken with dredges which collected the top two decimeters and a steel corer with plastic liner which sampled about the first half meter. The samples were air-dried immediately then sent for analysis by the Soil and Feed Testing Laboratory Department of Agriculture, Edmonton. The results are given in Table 3.

The sediment contains very little organic matter. Its nitrate level is low but phosphate frequently appears in more substantial amounts, but is essentially low. Phosphate levels are strongly stratified with the largest amounts present in the top 20 cm. The highest levels of phosphate have been found at depths below the photic zone. It is not known at present how available the phosphate retained in the sediments is for use by the plants. A large amount of calcium carbonate from snail shells and marl is present in the sediments.

Other areas in the lake, notably the eastern shores of Kapasiwin Bay and Goosequill Bay, have a firm bottom of clay with quantities of stones. These areas support only limited growth of submerged marcrophytes or

TABLE 3

Sediment Analyses of Lake Wabamun

Site[1]	Sampling depth[2](cm)	N	P	K	Fe	Na	pH	Exchange capacity
		ppm						meq/100gm
A	0-20	0.5	6.5	203	0.18	200	7.9	26.7
	0-50	-	-	-	-	-	-	-
B	0-20	2.5	35	187	1.25	200	7.0	27.7
	0-50	0.5	3.5	201	0.10	280	7.9	30.1
C	0-20	2	2	280	1.15	280	8.0	31.5
	0-50	0	1	217	0.18	280	8.4	27.5
D	0-20	0	1.5	133	0.30	100	8.1	15.9
	0-50	2.5	0	114	0.30	150	7.0	19.6
Centre of Lake	0-20	10	34	329	0.60	280	7.1	33.0
	0-50	7	17	245	3.55	280	7.0	-

[1]Sites A to D, described later under Study Sites, are under 3m of water. The centre of the lake site was under 6m of water. (Sites A to D shown in Fig. 9)

[2]Samples from 0-20cm taken with dredges. Samples from 0-50cm taken with corer.

are barren.

Dispersal of the Heated Effluents

The heated effluents from the power stations have two general effects; they increase the temperature of the water in an area of variable size and shape, and secondly, the increased temperature prevents ice formation in winter. Heating itself directly affects the physiological processes of the organisms exposed to it and the loss of ice cover results in an increased light flux during the winter with its own implications on the physiology of photosynthetic organisms.

The movement of water after it leaves the discharge canal is strongly influenced by wind-induced currents. Prevailing winds set up currents in the lake which are directed by the topography of the surrounding land and the lake's morphometry. As yet these currents have not been mapped but general trends can be seen from long-wave aerial infrared photography and by the shape of the ice-free areas in winter.

Several series of aerial infrared photographs have been taken of Lake Wabamun. Two photographs have been reproduced here through the courtesy of Professor J.B. Nuttall of the Department of Civil Engineering. Plate I shows the extent of the heated water in Kapasiwin Bay during a period of light southerly winds. On August 15, 1970 it shows that the heated water spread over the surface of almost all of Kapasiwin Bay. Two *Elodea* rafts are visible in the photograph, the more northerly one impeding the flow of warm water from travelling east, thus creating a "shadow".

Plate II shows the effect of strong northwesterly winds (on October 6, 1971) which create a current running west along the north shore. The heated water travels westward around Point Alison as far

PLATE I. Aerial longwave infrared photograph of Kapasiwin Bay showing the surface distribution of the heated water from the Wabamun power station on August 15, 1970 under the influence of light southeasterly winds (based on Edmonton Industrial Airport data). Lighter shades indicate temperatures. (Courtesy J.B. Nuttall)

PLATE II. Aerial longwave infrared photograph showing the surface distribution of the heated water from the Wabamun power station on October 6, 1971 with northwesterly winds (based on Edmonton Industrial Airport data). Flow is in a westerly direction close to the north shore. (Courtesy J.B. Nuttall)

as Riche's Point where it is deflected out into the lake and dissipated.

An isothermal map showing the distribution of heated water from the Wabamun Power Station for August 12, 1970 has been prepared by Professor Nuttall. This depicts the surficial patterns during a light northeast wind (Fig. 3).

The temperature of the discharge water is high enough to prevent ice formation in areas near the canals throughout the winter. In other areas the ice and snow cover is variable or reduced in thickness. The size of an ice-free area is influenced by the prevailing air temperatures. A period of warm weather brings about its enlargement. Figures 4 and 5 show the shapes of the open areas at the Wabamun and Sundance stations on different dates. At Wabamun the open water frequently extends around Point Alison to the intake canal indicating circulation in this direction even in winter. Plate III of the Wabamun open area taken on March 20, 1973 shortly before the break-up of the ice shows a flow pattern along the north shore very similar to that seen in Plate II. The surface temperatures within this flow near Riche's Point were only $4^{o}C$. A similar flow pattern along the north shore was photographed by Dr. J.R. Nursall in March 1970. This pattern of current movement appears to be one of fairly general occurrence.

Both the infrared photographs and the ice-free areas show only surface conditions. In winter, strong stratification occurs near the canals; the thermocline often lies only a few centimeters below the surface. Bottom temperatures even quite close to the discharge canals remain at $4^{o}C$. This implies that the importance of the heated effluents in the winter lies mainly in the reduction or elimination of the ice cover, not in raising the temperature of the water

FIGURE 3. Surface temperatures at the discharge canal of the Wabamun power station on August 12, 1970. (Courtesy J.B. Nuttall)

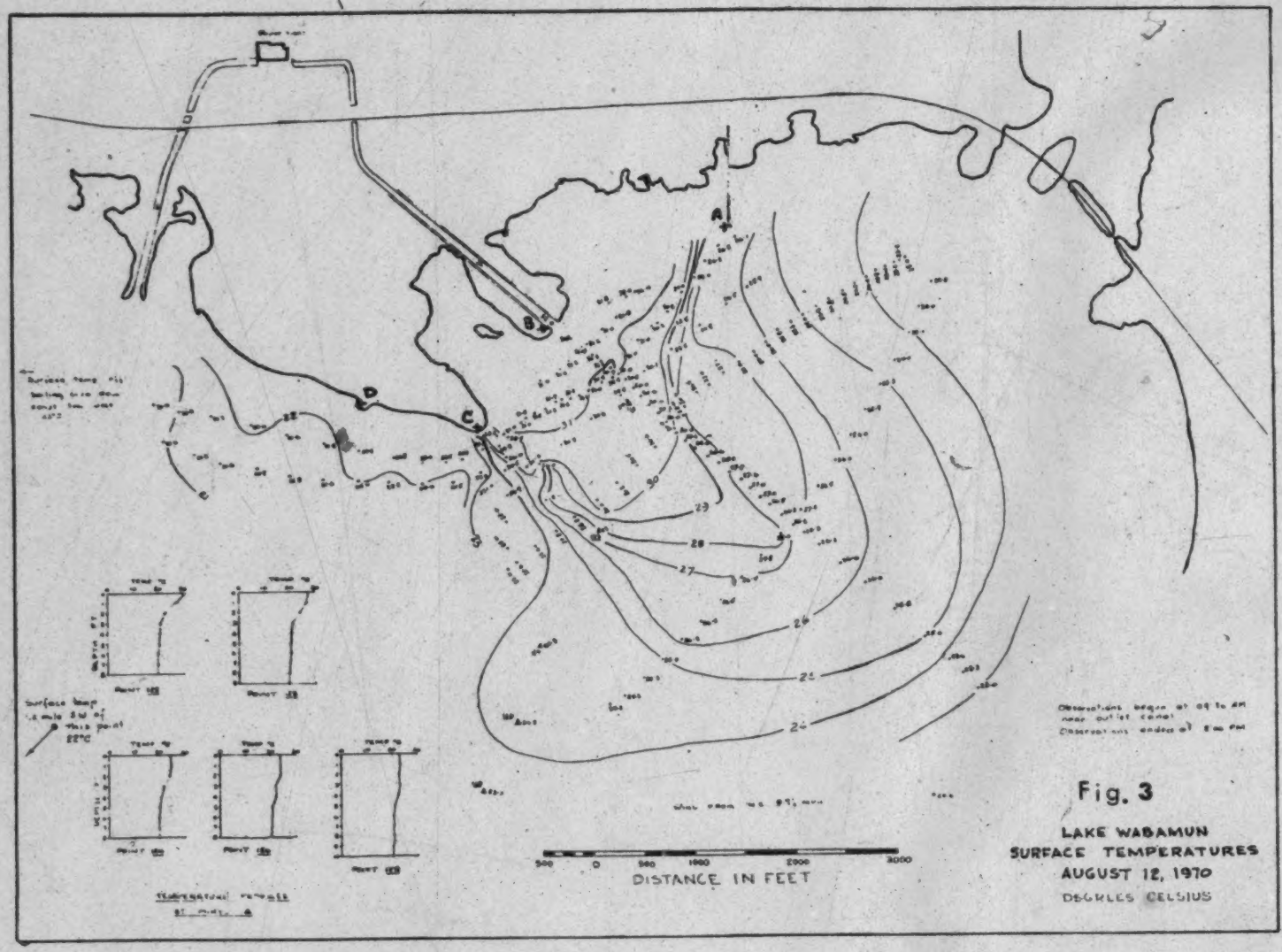


Fig. 3

LAKE WABAMUN
SURFACE TEMPERATURES
AUGUST 12, 1970
DEGREES CELSIUS

FIGURE 4. Ice-free areas produced by the Wabamun power station during the winter of 1970-71.

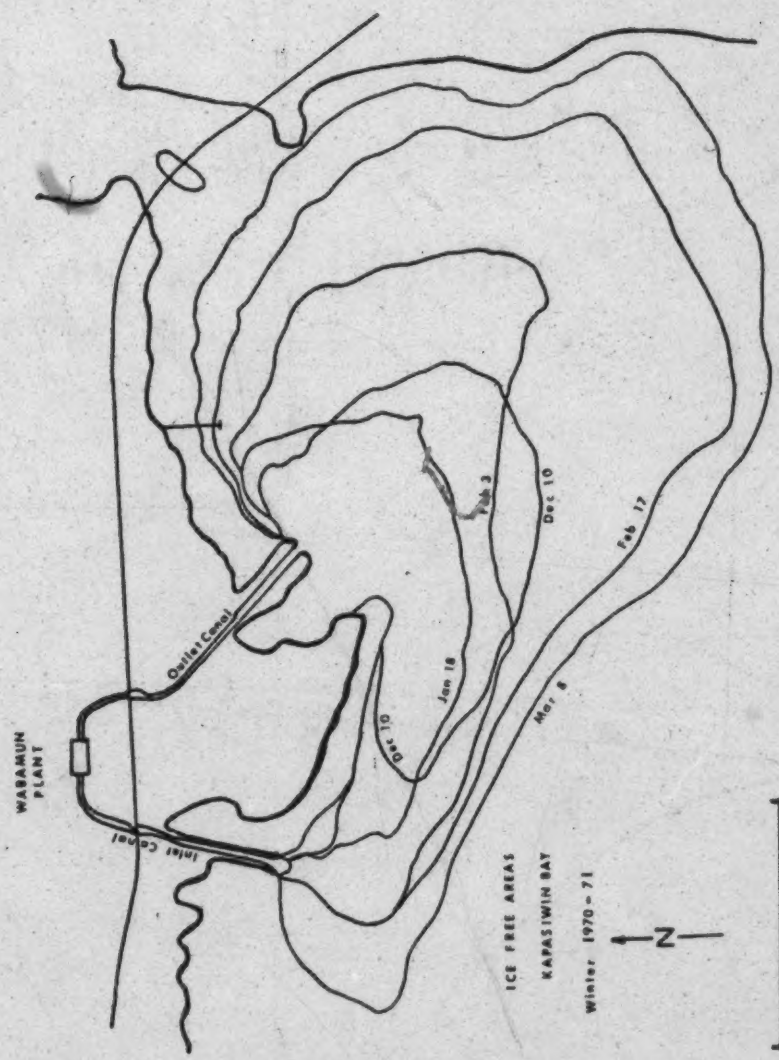

WABAMUN PLANT
Outlet Canal
Inlet Canal
Dec 10
Jan 18
Feb 3
Dec 10
Feb 17
Mar 8
ICE FREE AREAS
KAPASIWIN BAY
Winter 1970 - 71
N
1 km

Fig. 4

FIGURE 5. Ice-free areas produced by the Sundance power station during the winter of 1970-71.

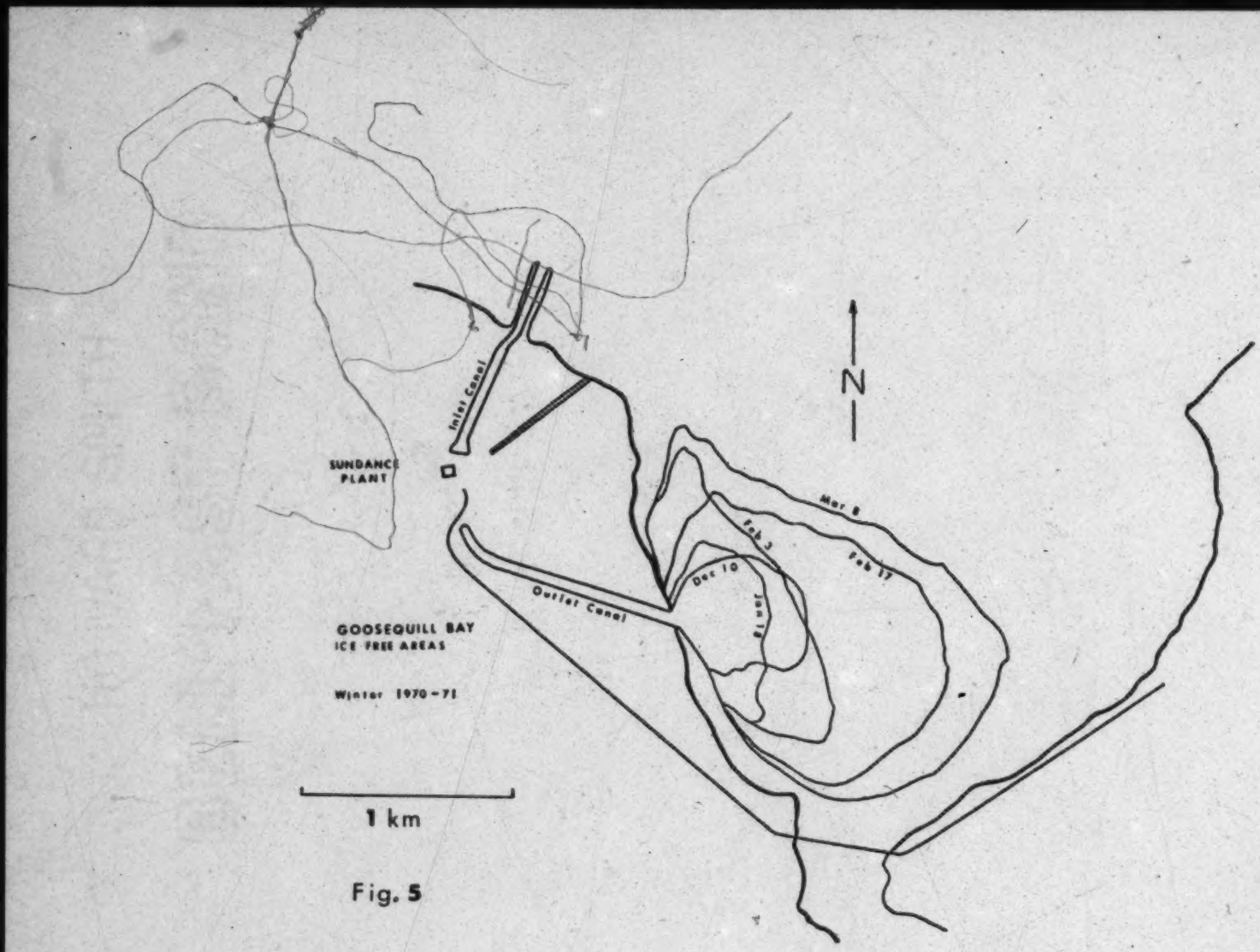
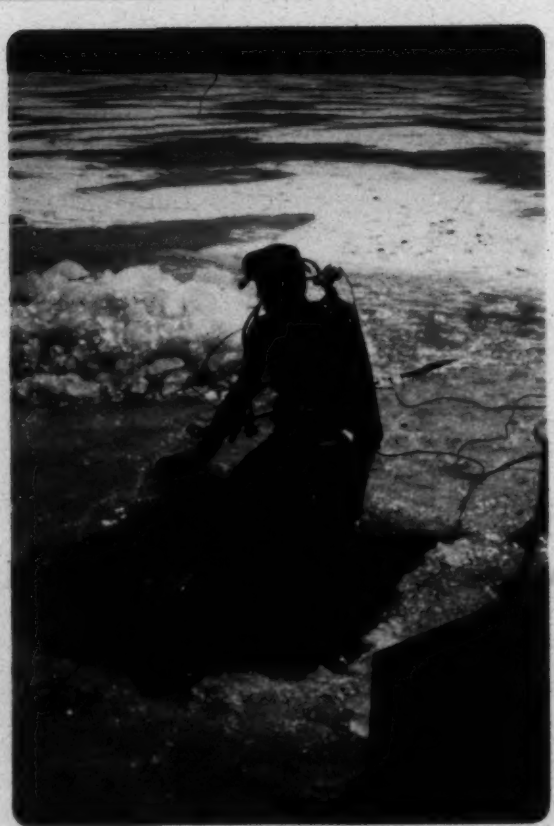

Inlet Canal
SUNDANCE PLANT
N
Mar 8
Feb 3
Feb 17
Dec 10
Outlet Canal
Power
GOOSEQUILL BAY
ICE FREE AREAS
Winter 1970 - 71
1 km

Fig. 5

PLATE III. Aerial view of the western edge of the ice-free area produced by the Wabamun power station on March 22, 1973 about 2 weeks before ice break-up.

PLATE IV. Measuring spectral intensities under the ice with a waterproof spectroradiometer. April 7, 1973.



surrounding the plants.

The dispersal of heated effluents in Goosequill Bay in relation to meteorological conditions is poorly understood at the present time.

The Light Regime of Lake Wabamun

Light intensity, light quality and the length of exposure affect the growth of plants. In a lake, the light reaching the plants is affected by the water surface which causes losses through reflection, by scattering due to particulate matter in suspension, and by absorption by the water and solutes.

Light quality in Lake Wabamun was determined with an Instrument Specialities Co. spectroradiometer which was enclosed in a water-tight housing. The instrument and housing were kindly made available by Dr. R.G. Wetzel, Director, Kellogg Biological Station, Michigan State University. The instrument measures spectral intensity over a wavelength range of 390 to 750 mm and the output from the instrument is recorded on a strip chart recorder. The housed instrument and recorder were calibrated against a G.E.C. lamp in an I.S.C.O. calibrator. Measurements were made by lowering the instrument to the desired depth where the waveband was scanned.

Measurements were made on March 31, 1973 in open water on a clear day. Scans were made in the air, and at a number of depths. The spectral intensities of sunlight and in the water column for this date are given in Fig. 6.

Measurements were made under 0.5m of ice on April 7,1973 (Plate IV). At this time there was very little snow cover on the ice, and the ice was becoming opalescent with air. The instrument was towed by a diver approximately 6m from the hole.

FIGURE 6. Spectral distribution in the water column measured with an I.S.C.O. spectroradiometer on March 31, 1973 at 1200 to 1300 hours M.S.T. with a slightly hazy day.

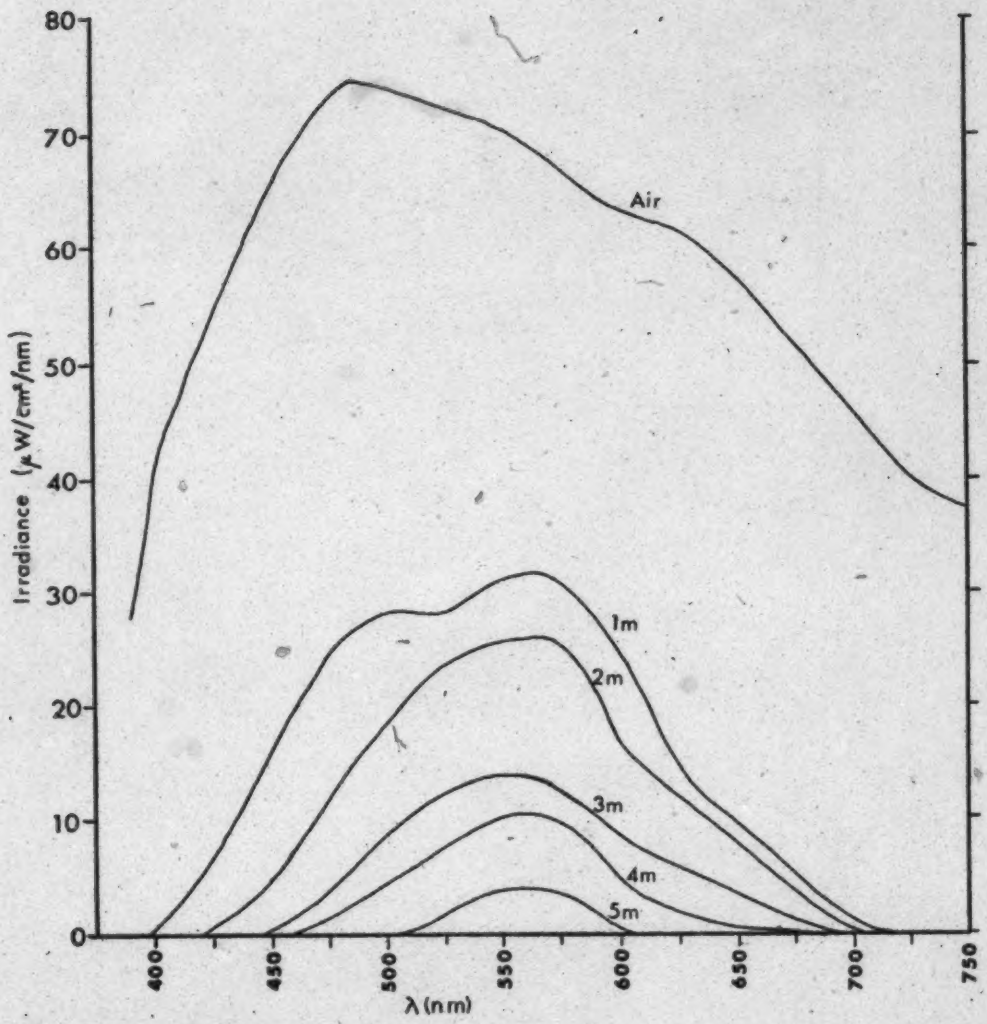

Irradiance (μW/cm²/nm)
λ(nm)
Air
1m
2m
3m
4m
5m
0
10
20
30
40
50
60
70
80
400
450
500
550
600
650
700
750

Fig. 6

Readings were taken immediately below the ice and 2m beneath the lower surface of the ice (Fig. 7). In open water, blue and red light are lost rapidly with increasing depth leaving green-yellow light with a maximum spectral intensity at 560 nm. This colour is typical of most lake water which is fairly rich in organic material. Similar curves have been published by Sauberer (1939).

Measurements taken under the ice showed that the ice acted as a light diffuser and caused little change in the spectral composition of the light passing through it. Blue light, especially, did not undergo as much absorption by the ice as by lake water of a comparable thickness.

Attenuation of light in Lake Wabamun has been measured using three different instruments. The I.S.C.O. spectroradiometer, a Lambda Instrument Co. light meter equipped with a cosine-corrected quantum sensor measuring a waveband of 400 to 700 nm, and an unfiltered opal-covered selenium photocell.

Attenuation (extinction) coefficients, E, were measured with the spectroradiometer at 450, 550, 625 and 675 nm. The decrease in intensity with depth for each wavelength, together with the respective attenuation coefficient is given in Fig. 8a. The values of E were determined from the expression

$$E = \frac{\ell n Io - \ell n Iz}{z} \qquad (1)$$

where Io is the light intensity at the upper depth, Iz is the intensity at the lower depth and z is the difference between the two depths.

Diffuse attenuation coefficients, E', were measured using the Lambda quantum sensor according to the same equation. Light levels and their E' are given in Fig. 8b for March 31 and June 29, 1973.

FIGURE 7. Spectral distribution in the water column and under ice. Measured with an I.S.C.O. spectroradiometer on April 7, 1973 at 1000 to 1200 hours M.S.T. with a clear sky.

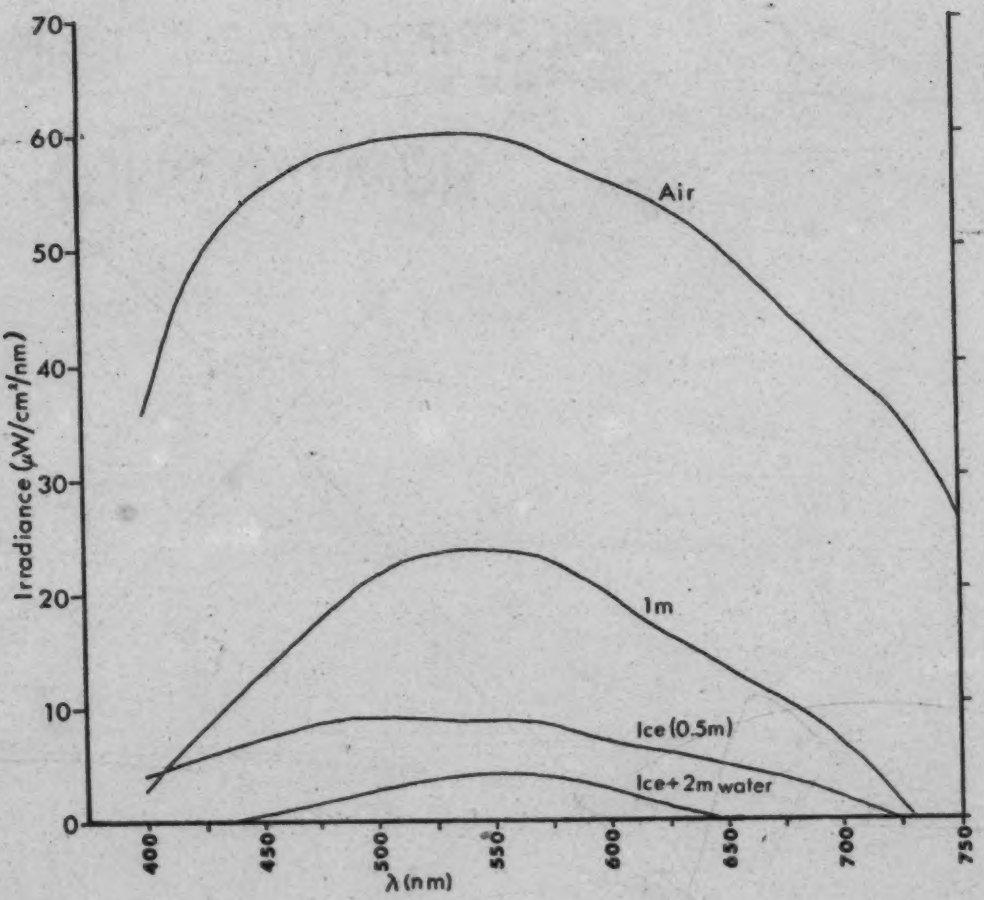

70
60
50
40
30
20
10
0
Irradiance (μW/cm²/nm)
Air
1m
Ice (0.5m)
Ice + 2m water
400
450
500
550
600
650
700
750
λ (nm)

Fig. 7

FIGURE 8. Light attenuation coefficients

(a) Measured at selected wavelengths with an I.S.C.O. spectroradiometer on March 31, 1973 (same conditions as Figure 6).

(b) Diffuse coefficients measured with a Lambda Inst. Co. quantum sensor (400 to 700nm) on two different dates. (μE = microeinstein).

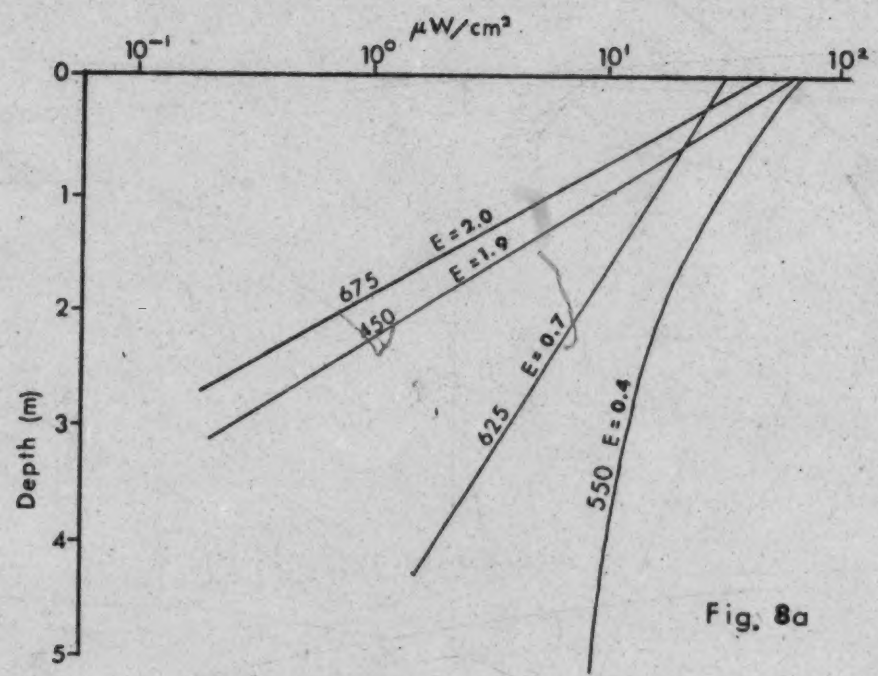

μW/cm²
10⁻¹
10⁰
10¹
10²
Depth (m)
0
1
2
3
4
5
675
E = 2.0
E = 1.9
450
625
E = 0.7
550
E = 0.4

Fig. 8a

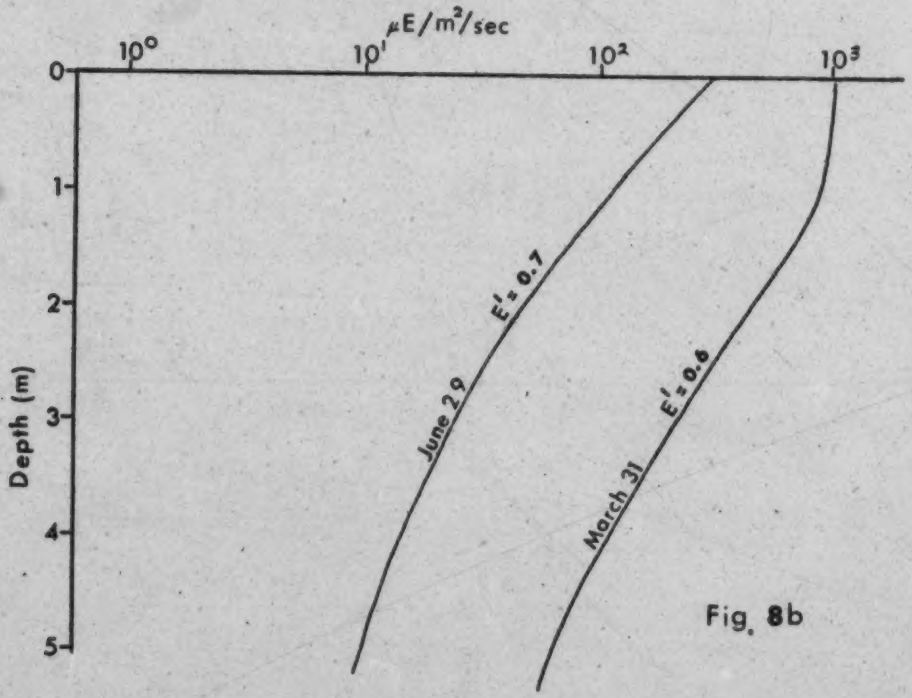

μE/m²/sec
10⁰
10¹
10²
10³
Depth (m)
0
1
2
3
4
5
June 29
E' = 0.7
March 31
E' = 0.6

Fig. 8b

Because the quantum sensor measures light over a waveband of 400 to 700 nm, changes in light quality affect its response. As the red and blue wavelengths are filtered out near the surface, the diffuse attenuation coefficient is high, but as the light becomes more monochromatic with depth, absorption becomes more constant and the attenuation coefficient decreases, causing the locus of the intensity vs. depth plot to curve downward. The diffuse attenuation coefficient was measured on several occasions and averaged about 0.7 in the winter and in the spring.

Light measurements taken with the selenium photocell under the ice surface were kindly made available by Mr. Leigh Noton of the Department of Zoology. The light loss due to several conditions of ice and snow cover was calculated from the equation:

$$\text{Attenuation factor} = \frac{1}{\frac{\text{light intensity above ice}}{\text{light intensity beneath ice}}} \qquad (2)$$

Attenuation of the light is due to the ice and to the snow cover on top of the ice. The transparency of ice decreases with age as the number of bubbles and inclusions increase. Transparency of snow also varies considerably, depending upon its water content and crystal size.

Both ice and snow depth are highly variable. The ice gradually increases in thickness throughout the winter while the snow depth does not necessarily follow any pattern. Warm periods and high winds may blow snow off the lake reducing its thickness and increasing its crystal size. As a result, the attenuation due to ice and snow varies tremendously. Some examples are given below:

	Attenuation factor
30cm snow & 68cm ice	7×10^{-4}
30cm snow with a layer of slush & 67cm ice	9.8×10^{-3}
Thin crust of snow & 70cm of spongy ice	9.6×10^{-2}
No snow, 48cm of spongy ice	0.16

From these figures it can be seen that the snow cover plays the greatest role in determining ice and snow attenuation.

The amount of light reaching a given depth can be roughly estimated from the surface light intensity, the ice and snow attenuation and the diffuse attenuation coefficient of the water.

In mid-winter with 68cm of ice and 30cm of snow giving an attenuation of 7×10^{-4} and an E' of 0.7, a surface light irradiance of 1500$\mu E/m^2$/sec would be reduced by the ice and snow cover to:

$$1500\mu E/m^2/sec \times 7 \times 10^{-4} = 1.05\mu E/m^2/sec$$

Using an equation derived from equation 1, the light at a depth of 4m of water below the ice would be reduced to:

$$I_4 = 1.05.e^{-0.7 \times 4} \qquad (3)$$
$$= 0.06\mu E/m^2/sec$$

which is an extremely low value. If the snow is reduced to a thin crust giving an attenuation of 9.6×10^{-2}, the irradiance at the bottom surface of the ice would be 144$\mu E/m^2$/sec. and at 4m below the ice it would be 8.8$\mu E/m^2$/sec.

STUDY SITES IN LAKE WABAMUN

Plant growth and development and phenology was monitored mainly at four sites. Their locations are given in Fig. 9. Two of the sites, B and D, were placed near the mouths of the discharge canals where they would come under the main influence of the heated water.

Site A was placed in cooler water in an established *Elodea* bed, and a control site, C, was chosen in an area where *Elodea* occurred but where the heating effect from the power stations was minimal. All sites were at a depth of 3m.

Site A is located South of the Wabamun pier. It has *Elodea* as its dominant macrophyte with traces of *Myriophyllum*. It is fairly strongly influenced by the heat from the Wabamun Station but the influence is highly variable and the site does occasionally freeze over in the winter.

Site B consists of a pure stand of *Elodea*. It is strongly affected by the heated water throughout the year under all wind conditions. The heating is strong enough to cause temperature stratification at all times.

Site C was established in an area where *Elodea* was present, but where the heating was minimal. The site is covered with ice for most of the winter but because of westerly currents along the north shore, the ice in the area melts prematurely in the spring. The site is populated with *Elodea*, *Myriophyllum*, *Potomageton vaginatus* in clumps and a bottom cover of *Chara*.

Site D was established near the mouth of the Sundance power station's discharge canal before the generator was commissioned in

October 1970. At that time the macrophytes occurring on the site consisted of heavy clumps of *Myriophyllum* and *P. vaginatus* with a continuous bottom cover of *Chara*.

Plant growth and their appearance at the sites was followed by sampling with a grapnel, by direct observation by diver and by photograph.

Early in the study, attempts were made to quantify plant growth by measuring biomass per unit area of bottom with the use of a $\frac{1}{4}m^2$ quadrat. The plants were then collected from inside the quadrat by a diver. The technique proved to be impractical because the plant size was so great that they became entangled with surrounding plants and the diver. The area around the quadrat quickly became riled and visibility was reduced to zero. Because of sampling errors and large variations in plant height and density, a large number of samples would have been required to obtain statistically representative data.

Plant heights were measured. This was most easily accomplished by diving but when this was impossible, plants collected by the grapnel were measured.

The best technique for obtaining a relative measure of biomass was accomplished by determining the dry weight of ten stems collected by diving whenever possible. Collecting by hand minimized breakage of the stems.

FIGURE 9. Locations of study sites.

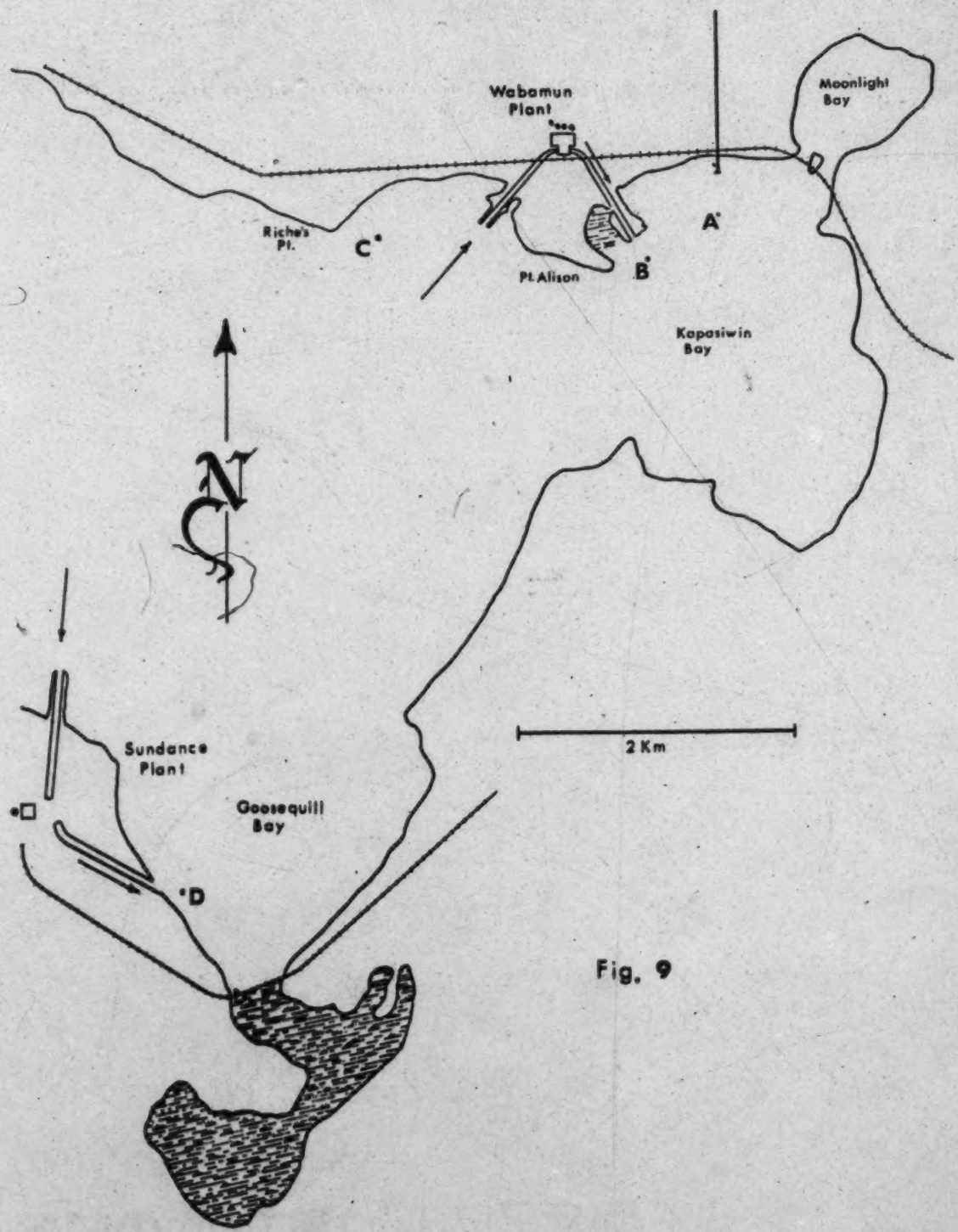

Wabamun Plant
Moonlight Bay
Riche's Pt.
C
A
Pt. Alison
B
Kapasiwin Bay
N
2 Km
Sundance Plant
Goosequill Bay
D

Fig. 9

INVASION AND SPREAD OF *ELODEA* AT THE SUNDANCE STATION (Site D and vicinity)

The plant community occurring in the area of the Sundance Station's discharge canal was mapped during the summer of 1970 prior to the commissioning of the first 300 Mw generator in late October. The power station operated intermittantly throughout the winter and was shut down for a 2-week period in August, 1971. The relation between power production and the temperature of the discharge water is given in Allen and Gorham (1973).

A number of changes were noted in the area of Site D during the summer of 1971. *Myriophyllum* did not achieve its usual densities and *P. vaginatus* was slightly reduced in abundance. The *Chara* understory appeared normal.

On September 9, 1971, inspection revealed that a large "hole" had been created in the *Chara* bed adjacent to the canal mouth which included Site D. The area had been denuded of *Chara*, and numerous clumps of *Elodea* 20-25 cm high had become established. The *Chara* immediately outside this area was sickly in appearance and the *Myriophyllum* and *P. vaginatus* remaining in the "hole" was covered with detritus. Considerable turbidity originating in the discharge canal had been noted in late August. The extent of the *Elodea* invasion about one month later, on October 2, 1971, was mapped at which time it occupied three acres. The *Elodea* colony was mapped three times subsequently and showed a rapid increase in area during the following summer (Fig. 10).

The sudden destruction of *Chara* in September was attributed to heating effects coupled with low light levels brought about by turbidity and the normal seasonal reduction in the number of hours of direct

FIGURE 10. Areas in the vicinity of the mouth of the Sundance discharge canal densely occupied by *Elodea*. Mapped on October 2, 1971, July 20, 1972, September 29, 1972, and July 4, 1973. Acreage shown indicates total area occupied.

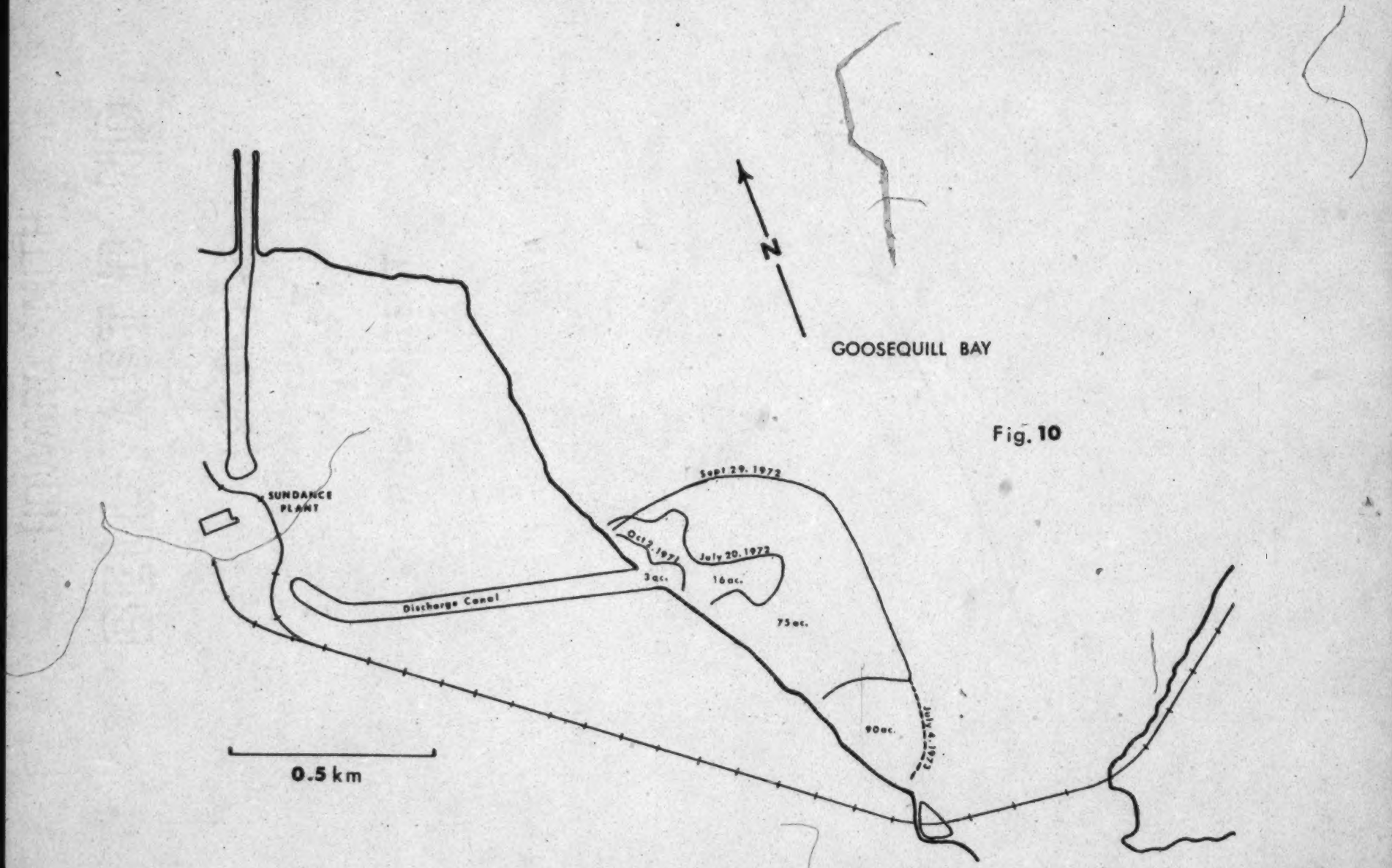

N
GOOSEQUILL BAY
SUNDANCE PLANT
Discharge Canal
Sept 29, 1972
July 20, 1972
Oct 2, 1971
3 ac.
16 ac.
75 ac.
90 ac.
July 6, 1972
0.5 km

Fig. 10

sunlight which combined to reduce net assimilation of carbon below compensation long enough to deplete the plants' reserves. A more detailed description has been published by Allen and Gorham (1973) and they have postulated that a similar type of invasion occurred in Kapasiwin Bay possibly following the commissioning of the (300 Mw) unit at the Wabamun Station in the winter of 1966-67.

At the time of the first survey in 1970 most of Kapasiwin Bay was already occupied by *Elodea*. Since that time, *Elodea* has moved into Moonlight Bay. Isolated clumps were first detected in August, 1972. To date (July 1973), *Elodea* in Moonlight Bay has not displaced the original species but has simply mingled with them. Since Moonlight Bay is connected to the rest of the lake by only a narrow channel, it does not receive any significant heating from the Wabamun Station and remains frozen throughout the winter. Under the conditions present in Moonlight Bay, it would appear that much of *Elodea*'s competative advantage is not realized.

SLOW SPREAD OF *ELODEA*

Elodea is able to spread beyond the original area of invasion by a slower process of infiltration and colonization. Large numbers of fragments from the main bed are carried from the area by currents and establish new plants. Such propagules have been found over the entire eastern end of the lake, some taking root at depths of 6.5m.

For colonization to occur at a great distance from the main bed, it must be large and dense enough to act as an intense source of inoculum.

The slower colonization is characterized by *Elodea* growing as individual plants rather than as clumps. The original species are not immediately displaced but they may gradually be choked out with the passage of a few seasons. The spread of *Elodea* in Kapasiwin Bay may have partly occurred in this way.

PHENOLOGY

The seasonal development patterns and methods of proliferation play an important role in determining whether a plant is capable of surviving in a given environment. In many submerged aquatic plants sexual reproduction if of little importance. In Alberta, for example, *Myriophyllum* flowers infrequently and few of the flowers that form produce mature fruit. *Elodea canadensis* is dioecious. It may produce abundant flowers but only one sex is usually present in a given body of water (Sculthorpe, 1967). Only male plants have been observed in Wabamun so far. The Potamogetons, however, produce large numbers of seeds and these are probably a significant method of propagation. The seeds are strongly dormant and require a low temperature treatment to germinate. Decomposition of the testa with time also aids in germination. Spence (1971) has shown that there is also a red light requirement.

In Lake Wabamun, particular attention was given to the formation of propagules by *Elodea* and *Myriophyllum* in heated and unheated areas.

In heated, ice-free water, *Elodea* passes the winter as sizeable plants which may be well over 1m high (Plate V). All of the plant is bright-green, healthy in appearance and growing as judged by periodic measurements. In late summer the new branches that are produced tend to have shortened internodes forming "winter tips" which have substantial quantities of starch. The amount of internode shortening or imbrication seems to be related to the average water temperature, with less occurring in warmer water (Plate VI). If these tips are removed from the parent plant during the winter, they tend to float. *Elodea* does not die back in the heated areas during the winter but considerable die-back does take place in the unheated

PLATE V. Underwater view of *Elodea*, showing the large standing crop near the mouth of the discharge canal of the Sundance power station. February 10, 1973. Plants about 70 cm tall.

PLATE VI. Winter tips of *Elodea canadensis* showing the effect of water temperature on their morphology. Left to right:

Warm water near Wabamun discharge canal (Site B)

Cooler water near Sundance discharge canal (Site D)

Cold water under ice at the control site (Site C).

Note short internodes of winter tip in contrast to to long internodes of parent stem.

April, 1971.

areas covered by ice and snow.

Shortly after the ice break-up,which generally occurs in mid-April along with rapidly increasing hours of direct sunlight, macrophyte growth begins. In the heated areas, *Elodea* elongates even more rapidly and flowering begins in the most heated areas by mid-May. The time at which flowering occurs in *Elodea* appears closely linked with the temperature to which it is exposed. Assuming a constant water depth, plants growing closest to the discharge canal flower earliest while those at a greater distance flower over a month later. Flowering may not occur at all in unheated areas such as the control site, C. In early spring, many of the winter tips produce roots at the nodes and at the same time, the stems become brittle. Breakage readily takes place and the tips float away. These floating cuttings or propagules, complete with roots are quite abundant in the eastern end of the lake throughout May and June (Plate VII).

Myriophyllum also forms imbricated winter tips at the ends of its branches but late in the Fall. These are denser than water, sink to the bottom when the parent plant disintegrates and there overwinter in a dormant condition in both heated and unheated areas. Rooting of the winter-tips does not occur until the water warms sufficiently in late spring.

Winter tips of *Elodea* and *Myriophyllum* behaved similarly when they were warmed. Tips of both species collected in March rooted and began to elongate within three days when warmed to 18°C in the laboratory.

The large numbers of floating winter tips produced by *Elodea*,

PLATE VII. *Elodea* winter tips which had broken off and were found floating in the lake.Note presence of roots. March, 1971.

PLATE VIII. Fragments and tips of *Elodea* washing up on the ice at the edge of the ice-free area produced by the Wabamun power station. December 9, 1971.

and their high mobility make them excellent agents of propagation. They are released even in the winter from heated areas (Plate VIII) as well as in the spring and become established and begin to elongate before other species such as *Myriophyllum* and the Potamogetons break dormancy and so are able to shade competitors. Colonization can also occur in the fall when other species are in a debilitated condition. From field and laboratory observations it appears that the winter tips of *Elodea* require no exposure to low temperatures to initiate root development.

The seasonal development of *Elodea* is also affected in the heated areas. Plants in these areas overwinter very well with no die-back and enter the active growing season in a large, well-developed condition. They grow rapidly, flower and reach the surface earlier. When they reach the surface, usually in early July at Site B, they are essentially mature plants. They lose their bright green appearance, taking on an olive-green hue and the branch tips near the surface become reddish or partially bleached from the high light levels (Plate IX). The plants become senescent and because of their proximity to the surface, they are broken off near the base by wave action and float to the surface to form rafts, often of considerable size, which drift with the wind (Plate X). It is this characteristic that makes *Elodea* such an obnoxious weed in Lake Wabamun.

In contrast, *Myriophyllum*'s development is not significantly accelerated in the heated areas. It's overwintering tips are strongly dormant and do not root in the fall or late winter. *Myriophyllum* must therefore re-establish itself every spring from the winter tips produced during the previous fall.

PLATE IX. *Elodea* showing browning and senescence from an area in the main stream of the heated water from the Wabamun discharge canal (left) compared with non-senescent *Elodea* from a nearby area in cooler water (right). June 22, 1971.

PLATE X. Floating rafts of *Elodea* in Kapasiwin Bay. July 24, 1970.

Elodea in unheated areas re-establishes itself in the fall from tips or long, buried stems or stolons. Shoots may reach 0.5 to 1m in height before the lake freezes over. Its development pattern in unheated waters with ice cover more nearly resembles the seasonal development of the other macrophytes. The growth and phenology of *Elodea* at the heated sites and the control site is given in Fig. 11.

The phenology of *Myriophyllum* is essentially the same in the heated and non-heated sites, A and C, respectively. It may be summarized with dates (which will tend to vary somewhat from year to year) as follows:

May 15 - June	Elongation
June - September 15	Maturation
September 15 - November 15	Senescence; formation of winter tips
November 15 - April 15	Decay; winter tips dormant on bottom
April 15 - May 15	Winter tips break dormancy

The phenology of *Chara* and the Potamogetons was not studied in detail. However, no striking differences were noted between the heated and unheated sites.

PART II

NET ASSIMILATION EXPERIMENTS

FIGURE 11. Phenology of *Elodea* at two heated sites (A and D) and at the slightly heated control site (C).

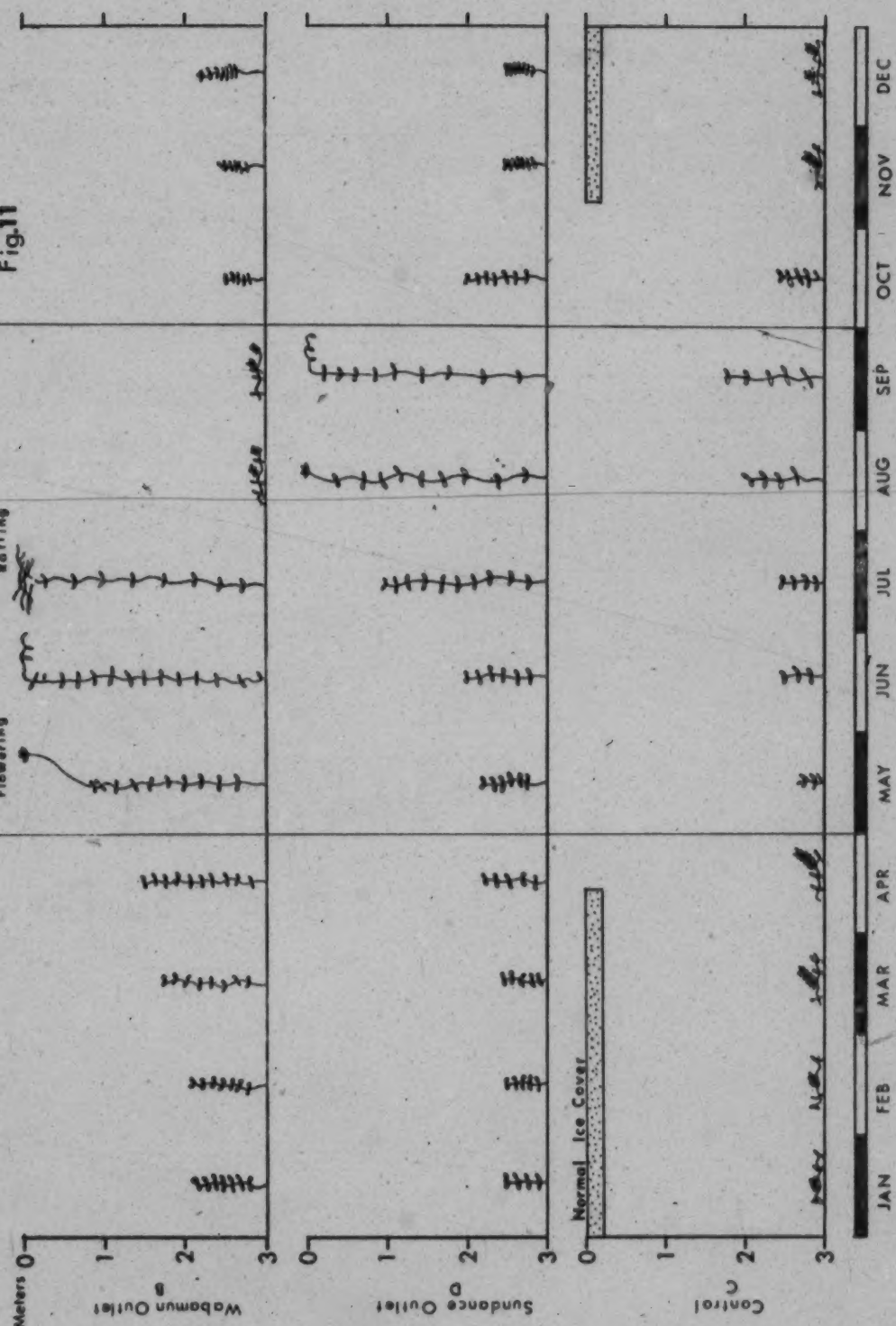


Fig.11
Meters
Wabamun Outlet
B
Sundance Outlet
D
Control
C
Flowering
Rafting
Normal Ice Cover
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC

MEASUREMENT OF NET ASSIMILATION

It was desired to determine how the four species of macrophytes performed under varying conditions of light, temperature and pH and how they compared with each other in their responses.

The response of a plant to a given set of environmental conditions can be measured in several ways such as increase in size, in weight or by its assimilation of carbon. The first two methods may require a prolonged period of time while the measurement of net assimilation is rapid and can provide a continuous record of a plant's metabolic activity.

Net assimilation can be measured directly by carbon dioxide uptake or indirectly by oxygen production. In an aqueous system, carbon dioxide or bicarbonate may be used by the plants. Uptake of carbon can be measured accurately only by using ^{14}C-labelled bicarbonate. This technique however does not allow continuous measurement. Oxygen production can be followed accurately by using a polarographic sensor which continuously measures the oxygen concentration in the water. The technique assumes that there is good diffusion of oxygen from the plant into the surrounding solution. All macrophytes with the exception of *Chara* have an extensive system of air spaces or aerenchyma which can act as a gas reservoir. When the aerenchyma is filled to capacity, oxygen leaves the plant either in solution or as bubbles when oxygen saturation of the surrounding solution is reached. Bubble formation can be greatly reduced by lowering the oxygen concentration of the surrounding solution to well below saturation. The formation of bubbles should be avoided because the oxygen which escapes is not measured.

SAMPLE COLLECTION AND STORAGE

Plant material for use in the net assimilation experiments was collected in Lake Wabamun and used as soon as possible after collection. Plants were stored in water in a growth chamber at 4°C with 16 hours of low light from 200W of incandescent lights. Air was bubbled through the water. All plants except *Chara* tolerated this treatment for at least 10 days. *Chara* was useable for 4 to 5 days after collection, but was generally used within 24 to 48 hours after collection. No conditions were found in which *Chara* would survive for long periods.

The plants collected were the healthiest and cleanest that could be procured. The terminal 5cm of *Chara* and 10-15cm of the other species were used. The plant material was washed to remove detritus. Some epiphytic algae, particularly diatoms, were present but plant material was chosen on which the epiphytic population was as low as possible.

After being used in a net assimilation experiment the organic weight of the plants was determined. The plants were oven-dried at 80°C for 18 hours, weighed and ashed. The ash weight was then subtracted from the dry weight to give the weight of combustible substances. The organic weight was deemed to be a better way of measuring the amount of plant material used, especially when comparing different species. The amount of ash on a dry weight basis varies considerably from species to species and may change during the year.

DESCRIPTION OF NET ASSIMILATION APPARATUS

All net assimilation experiments were performed in an Environmental Growth Chamber Co. reach-in chamber (Plate XI). The working space in this chamber measured 1m x 1m x 0.7m. The walls were of aluminum coated with mylar which helps to retain their high reflectivity. Temperature could be controlled over a range of -10 to 50°C. A large heat transfer capacity enabled the chamber to achieve a new temperature quickly.

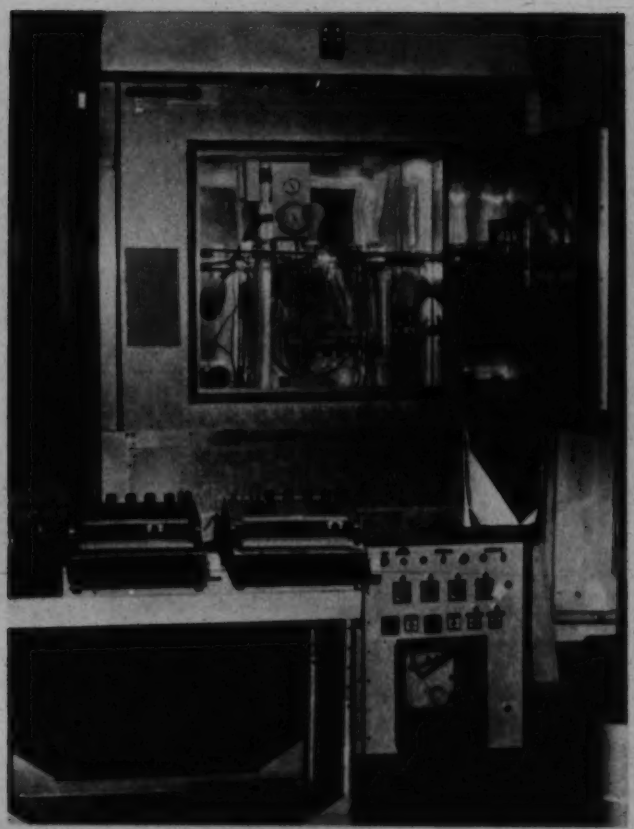
Lighting in the chamber consisted of two sets of lights, six 150-watt incandescent lamps and twenty cool white fluorescent lamps. The fluorescent lamps were not used. The incandescent lamps could be controlled in two groups consisting of 2 and 4 lamps each which could be used to give light settings of 1/3, 2/3 and 3/3. The lamps built into the chamber were supplemented with an additional bank of six 200-watt flood lamps and a single 150 watt bulb. The built-in lamps were located in a light cap which was water-cooled while the heat from the supplementary lamps was absorbed by four plastic water-filled cells two inches thick (Plate XII).

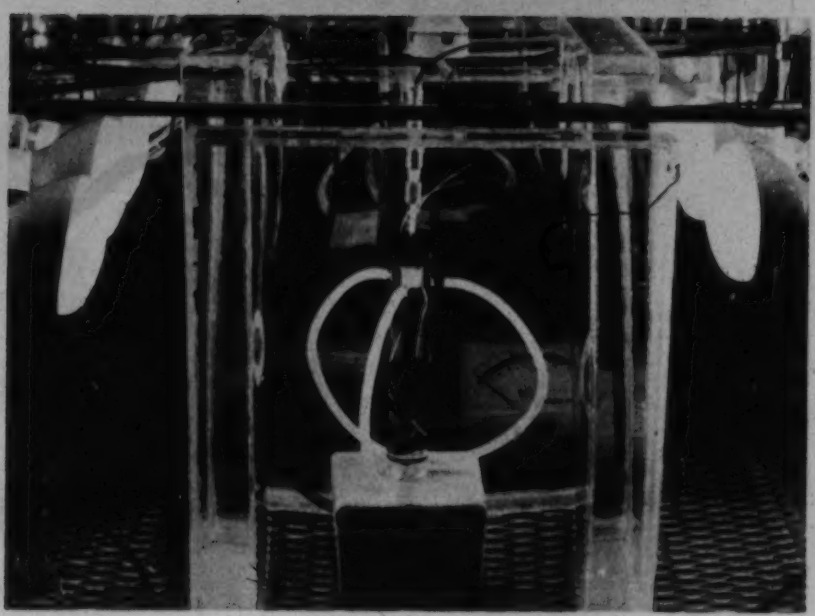
Two types of cuvette were used, one with a volume of 173ml for light and temperature experiments and a larger cuvette of 1.86 liters capacity for pH experiments.

The small cuvette was made from 3cmID clear plastic. It was fitted with three side arms of Tygon tubing (3/16" inside diameter). A small teflon-coated stirring bar was placed in the bottom and covered with a perforated plastic disc. In operation the stirring bar served as a centrifugal pump, drawing water down through the perforated disc and out through the side arms to the top of the

PLATE XI. Growth chamber used for net assimilation experiments. Shown with the small cuvette and chart recorders.

PLATE XII. Arrangement of extra lamps and heat absorbing cells in growth chamber. Shown with cuvette in place.





cuvette. This form of circulation provided a perfectly steady flow of water over the plants and the incoming streams from the side arms provided adequate flow over the membrane of the oxygen sensor (Fig. 12).

The oxygen sensor used was a Beckman polarographic oxygen electrode connected to a Beckman Fieldlab oxygen meter. The sensor was pushed through a rubber stopper which served as a top for the cuvette. A small thermistor bead epoxyed on the end of a glass tube was located beside the oxygen sensor. The oxygen meter was connected to a Heath Model EV-20B chart recorder and the temperature sensor to a Wheatstone bridge.

The large cuvette (Fig. 13) was also made from clear plastic tubing, 10.5cm in diameter, with a flange on the upper end also of clear plastic. The lid was a flat plastic disc held down by 8 bolts. Two short tubes were attached near the bottom of the cuvette. Through these an oxygen sensor and a coaxial pH electrode mounted in rubber stoppers could be inserted. Circulation was provided by a stirring bar. The plants were kept away from the stirring bar by a screen supported by a plastic ring on three legs. A number of glass rods attached to the lid prevented movement of the plants. The pH electrode was connected to a Radiometer pH meter which was equipped with a recorder connection that led to a second Heath recorder.

FIGURE 12. Apparatus used for the light and temperature experiments:

A - cuvette, volume 173ml

B - Tygon side-arms

C - Polarographic oxygen sensor

D - Thermistor temperature probe

E - Magnetic stirrer

F - Water-filled heat absorbing cells, 5 cm thick

G - 6 x 250-watt flood lamps

H - 6 x 150-watt light bulbs located in the light cap of the growth chamber

I - Single 150-watt light bulb.

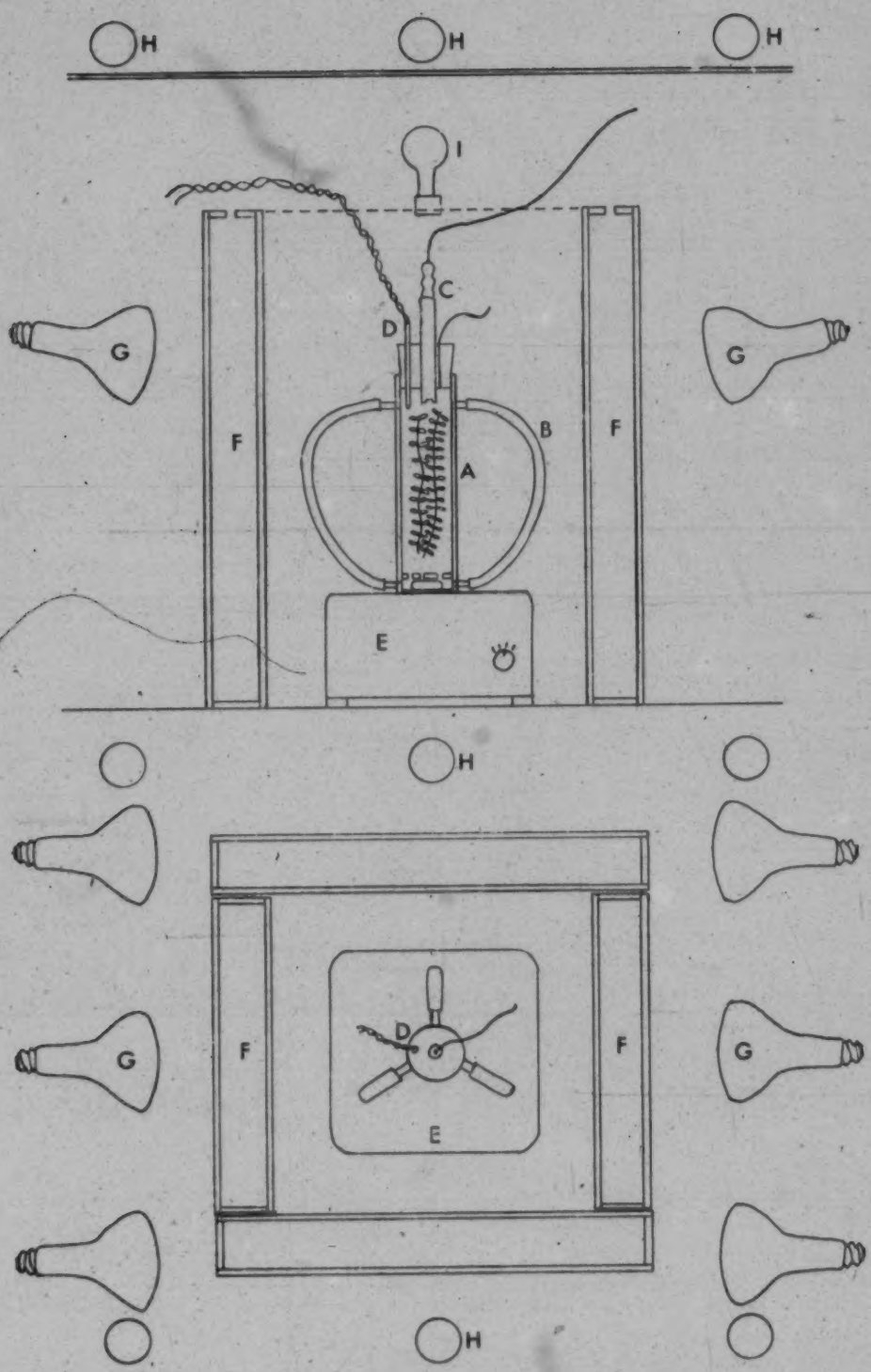


Fig. 12

FIGURE 13. Cuvette used for pH experiments - volume 1.86 liters.

A - Polarographic oxygen sensor

B - Coaxial pH electrode

C - Stirring bar

D - Magnetic stirrer

E - Screen

F - Glass rods to prevent plants from moving

G - Filling ports.

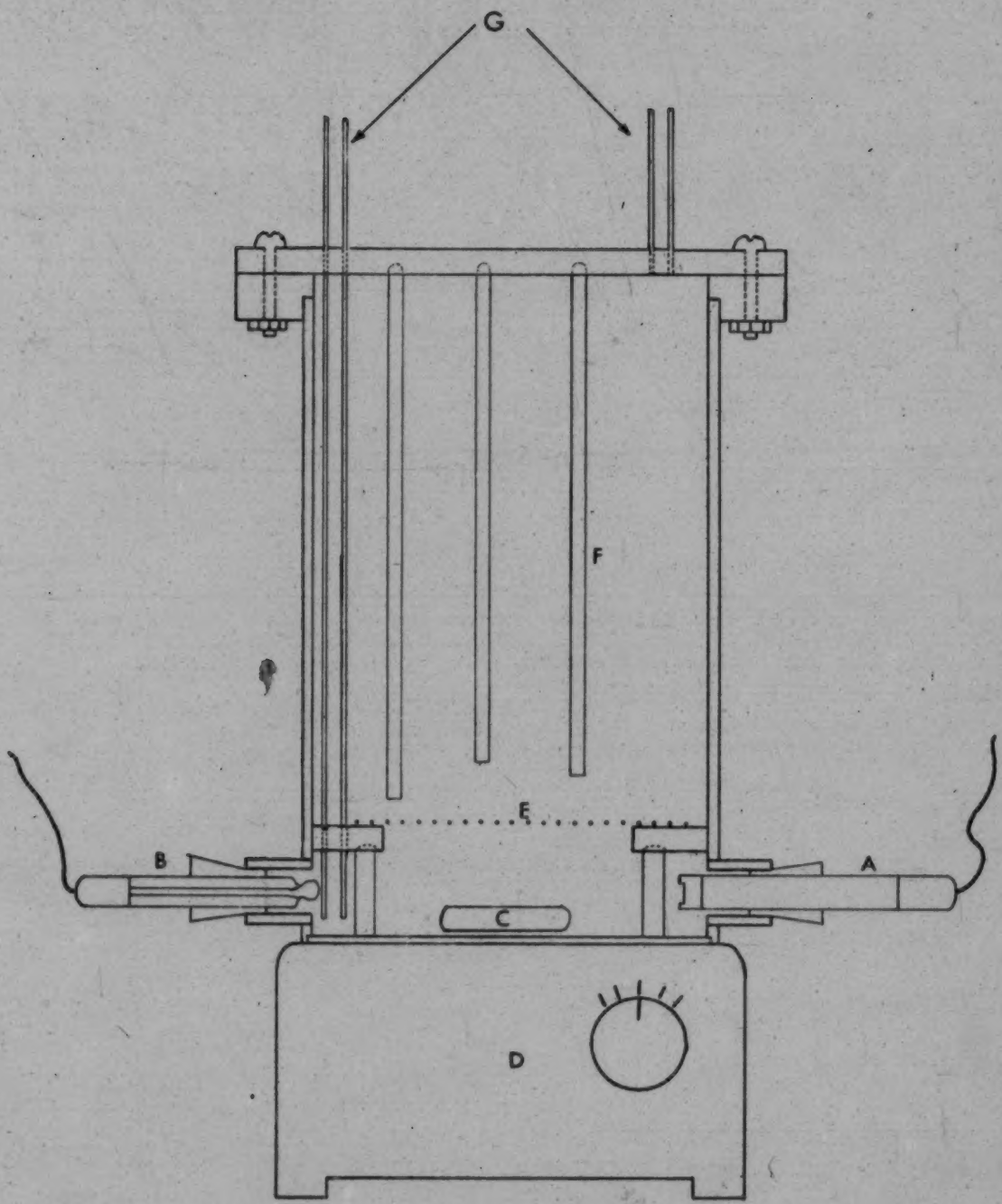


Fig. 13

CALIBRATION OF APPARATUS

The thermistor was calibrated against a good quality mercury thermometer and a graph prepared which converted the units from the Wheatstone bridge to degrees Celsius ($\pm 0.2^{o}$).

Light levels used in the net assimilation experiments were measured in micro-einsteins/ m^2/sec. A quantum sensor made by the Lambda Instrument Co. of Lincoln Nebraska was used. This sensor measured light over a waveband of 400 to 700nm. One einstein corresponds to 1 mole of quanta. The mean wavelength measured by the sensor is 575nm. One $\mu E/m^2/sec$ corresponds to 20.82 $\mu W/m^2$ at 575nm.

The light field inside the small cuvette was measured with a small silicon photocell mounted on the end of a piece of glass tubing which was bent through a right angle. The photocell was connected through a voltage divider to a Heath recorder. The photocell's output was calibrated against the Lambda Instrument Co. quantum sensor using several levels of incandescent light. A graph was then prepared which converted the output of the photocell to $\mu E/m^2/sec$. This graph was valid for incandescent light only.

Light measurements inside the cuvette were obtained by placing the photocell probe into the water-filled cuvette and adjusting the lights to all the practical combinations. The photocell was then rotated through an angle of 90^{o} and the series of light measurements repeated. This was done at 90^{o} intervals for a full circle. At each light level the four measurements which described the light field were averaged and converted to $\mu E/m^2/sec$. The whole procedure was repeated at frequent intervals. Light combinations were chosen which gave a good range of light levels for use in the experiments.

The oxygen meter was calibrated using a standard of air-saturated water. The oxygen concentration at a given temperature was taken from a table by Truesdale, Downing, and Lowden (1955).

PROTOCOL OF EXPERIMENTS

Light-temperature experiments were carried out in water containing 1000ppm of bicarbonate (as potassium bicarbonate). This solution was stored in a growth chamber at 4°C with the plants. Before the experiment, the solution was de-oxygenated by bubbling nitrogen through it. The oxygen concentration was reduced to about 1ppm. A quantity of washed plants was put in the small cuvette and the bicarbonate solution poured in. The amount of plant material used (0.1 to 0.5g dry wt) was enough to give good rates of oxygen production without being so crowded as to cause self shading. This was determined only through experience. The plants were evenly spread in the cuvette with forceps, and the cuvette placed on top of the stirrer in the growth chamber set at 5°C. The pH was then measured and adjusted to 8.1 with hydrochloric acid. The stopper carrying the oxygen sensor and thermistor was inserted and the electrical connections made. The cuvette was then allowed to "settle in" in complete darkness for about 30 min. The latter part of this dark period was used to measure the rate of respiration, designated R_1.

The cuvette was exposed to the lowest light level first, followed by increasing intensities. After the highest intensity, the light was turned off and the final respiration rate, designated as R_2, was measured.

After completion of the run at 5°C, the temperature was changed to 15°C. The water in the heat-absorbing cells usually cooled enough during the course of the experiment to cause fogging when the air temperature of the chamber reached the temperature of the cells. This condition was alleviated by pumping hot water into the cells while

withdrawing cool water at the same rate. The cuvette was allowed to come to temperature, the oxygen concentration lowered with nitrogen, and the pH re-adjusted to 8.1. After "settling in" the light series was repeated. The entire operation was again repeated at 25°C.

Upon completion of the light-temperature response measurements, the organic weight of the plants used in the experiment was determined.

The pH experiments were carried out in the large cuvette at 20°C at a fixed light level (approx. 25μE/m^2/sec) in a solution containing 600ppm of bicarbonate at pH 8.3. The pH was adjusted upward in steps with sodium hydroxide to pH 10.6 and downward in steps to pH 5 with hydrochloric acid.

During the course of an experiment, the rate of oxygen production was recorded. This rate was determined by measuring the slope of the line drawn on the strip chart and expressing it as ppm O_2 produced per hour. The rate was then multiplied by a constant derived from the volume of the cuvette divided by the organic weight of the plant material. This gave net assimilation in mg O_2/hr/gm. The rate of oxygen production was not altered by the addition of calcium and/or magnesium ions.

RESULTS

Light and Temperature Experiments

The apparatus used to measure net assimilation and respiration of aquatic macrophytes proved to be remarkably responsive to the dissolved oxygen exchange of plants. A change in the light level generally produced a change in the oxygen production rate within 1 to 3 minutes. The slopes obtained in the light on the chart recorder were usually very straight even over lengthy periods of time, indicating that net oxygen production and its diffusion from the plant into the surrounding water was constant. The respiration rates obtained in the dark were not constant and gave curved lines on the chart. The rate of respiration was highest immediately after exposure to light and gradually diminished with time. The rate of oxygen consumption continued to diminish until the available oxygen was totally depleted.

Gas trapped in the aerenchyma did not produce any serious problems. If the plants were kept in the dark they used up most of their stored oxygen. When these plants were illuminated, it took several minutes for oxygen to be released into the surrounding water. This lag period varied inversely with the light intensity to which they were exposed. During the lag period there was no net oxygen exchange with the water giving the appearance that the plant was light compensated. Since nearly all the photosynthetic cells are in direct contact with the external solution the lag period possibly represents the time taken for the oxygen to reach concentrations within the cell where it will begin to diffuse out rapidly. During this time the respiratory needs of the cell are met from internal sources so oxygen is not taken into the cell from the outside.

The net assimilation rates produced by the four species under different conditions of light and temperature at a pH of 8.1 are shown in Fig. 14 and the respiration rates over the temperature range of 5^{o} to 25^{o}C are given in Fig. 15. The curves shown are derived from six or more experiments. In Fig. 14, a reference line has been drawn through the 40 $\mu E/m^2$/sec irradiance level to enable comparisons of net assimilation rates at light-limiting levels to be made more easily. Depending upon season and cloud cover this level of irradiance occurs at some depth between 1 and 5 meters in waters similar to Lake Wabamun with an E' of 0.7.

pH Experiments

Two types of pH experiment were carried out. The major series of experiments were performed at low light levels (25 $\mu E/m^2$/sec) using a solution containing 600ppm bicarbonate (at pH 8.3) at a temperature of 20^{o}C. The large cuvette was used as it provided a large volume of solution whose pH was more stable while the plants were photosynthesizing. Rates of net assimilation at various pH values were plotted as percentages of the maximum rate attained. Figure 16 shows how the four species examined performed under differing pHs. The pH range 8.5 to 10 which covers the pH values most frequently found in Alberta lakes has been marked on the graph.

A second experiment was performed in which a quantity of *Myriophyllum* was exposed to conditions of low and high light (25 and 260 $\mu E/m^2$/sec) and to low and high concentrations of bicarbonate (50 and 600ppm at pH 8.3) while the pH was varied. The results were plotted in two ways; first as percentages of the maximum rate attained and second, in absolute rates of net assimilation (Fig. 17a, b)

FIGURE 14. Net assimilation rates for *Elodea canadensis*, *Myriophyllum exalbescens*, *Chara globularis* and *Potamogeton pectinatus* at three temperatures expressed in mg of oxygen per hour per gm of organic material. Light levels are in $\mu E/m^2/sec$ (400-700nm); the lines at 40 are for reference.

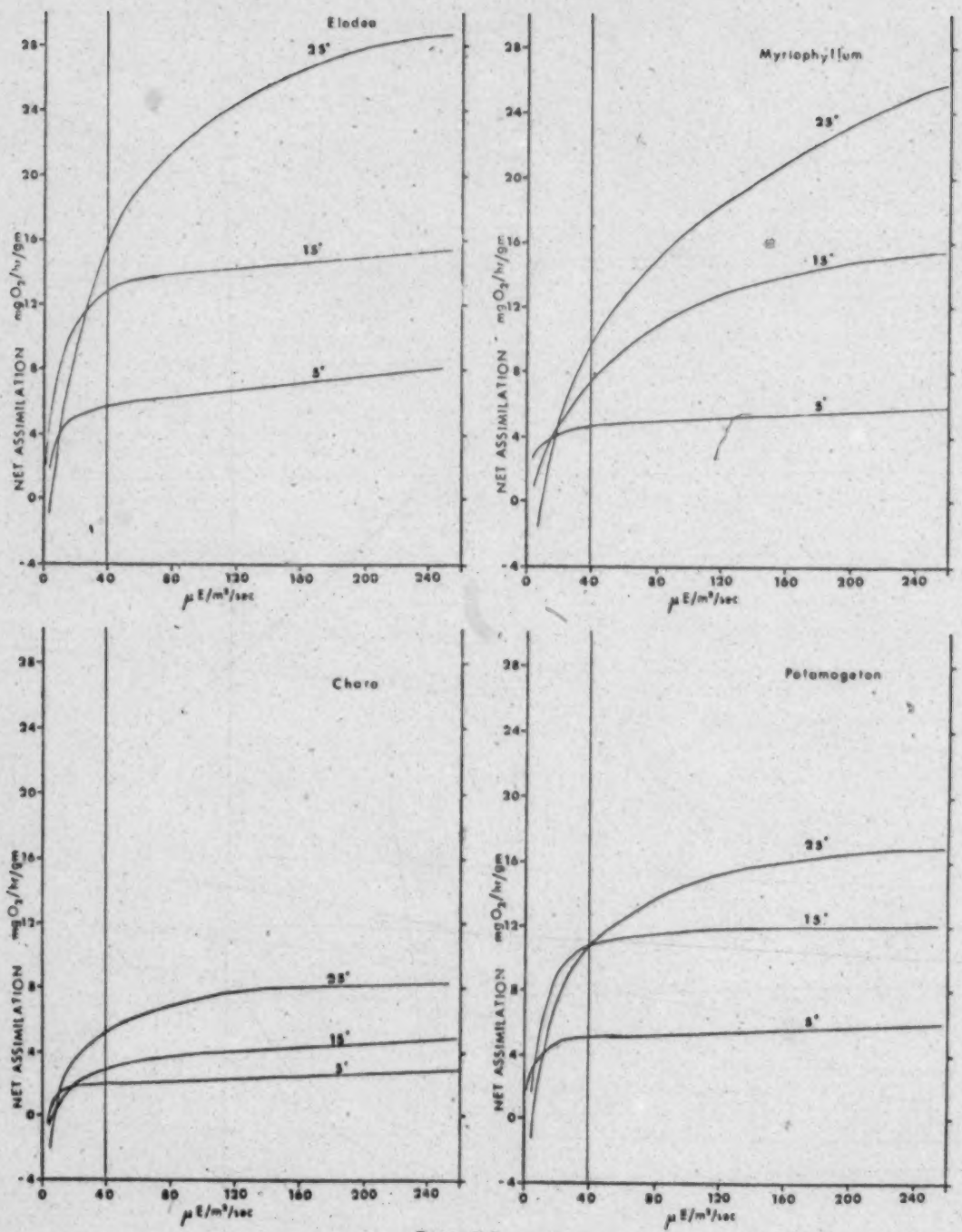

Elodea
Myriophyllum
Chara
Potamogeton
25°
15°
5°
NET ASSIMILATION mgO2/hr/gm
μE/m²/sec
-4
0
4
8
12
16
20
24
28
40
80
120
160
200
240

Fig. 14

FIGURE 15. Respiration rates for *Elodea canadensis*, *Myriophyllum exalbescens*, *Chara globularis* and *Potamogeton pectinatus* over the range of 5-25^{o}C expressed as mg of oxygen per hour per gm of organic matter.

R_1 is the rate after being kept in the dark for 30 minutes

R_2 is the rate immediatly after exposure to high light intensities (260μE/m^2/sec.).

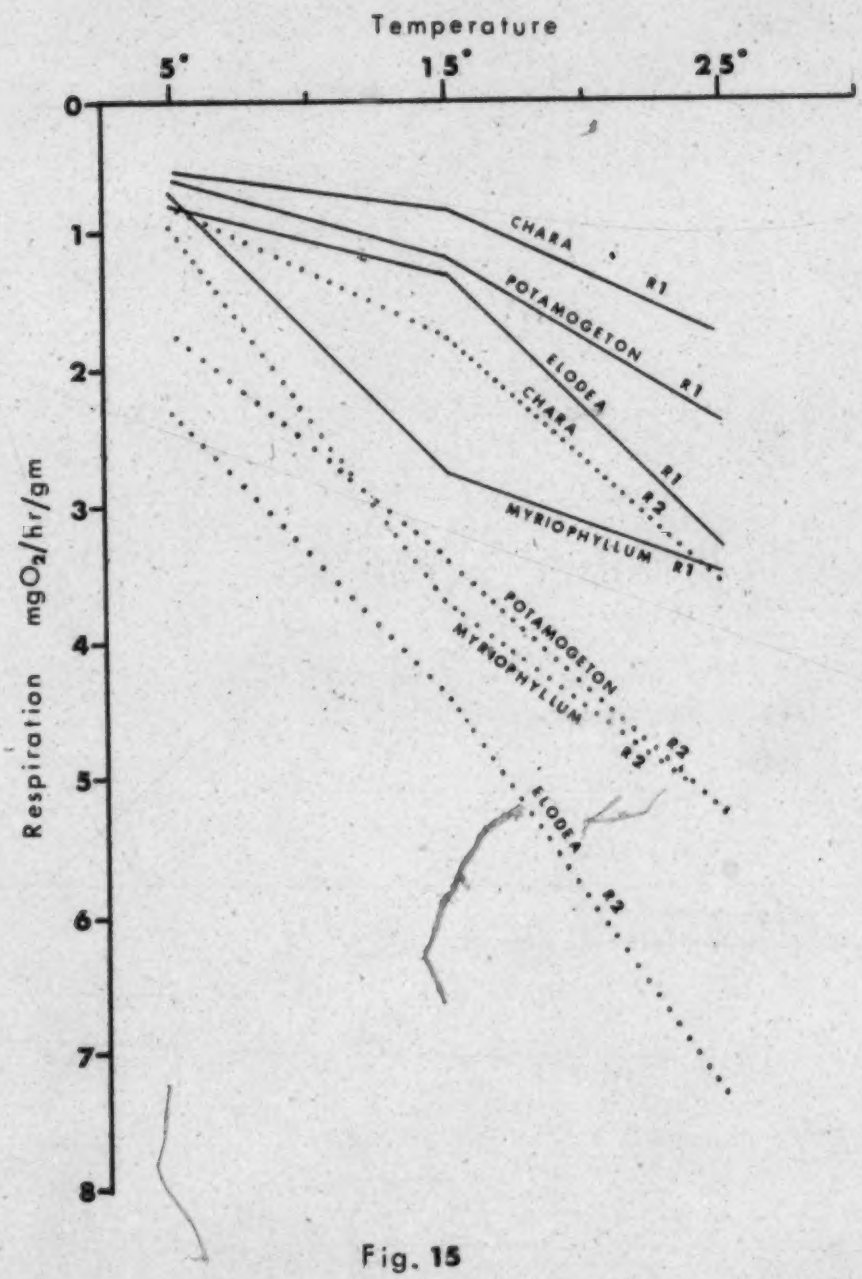

Temperature
5°
15°
25°
0
1
2
3
4
5
6
7
8
Respiration mgO2/hr/gm
CHARA R1
POTAMOGETON R1
ELODEA R1
CHARA R2
MYRIOPHYLLUM R1
POTAMOGETON R2
MYRIOPHYLLUM R2
ELODEA R2

Fig. 15

FIGURE 16. Effects of pH on rates of net assimilation for *Elodea canadensis*, *Myriophyllum exalbescens*, *Chara globularis* and *Potamogeton pectinatus* under conditions of limiting light and 600 ppm of bicarbonate (at pH 8.3) expressed as percentage of the maximum rate attained. Typical pH range for Alberta lakes is indicated by reference lines.

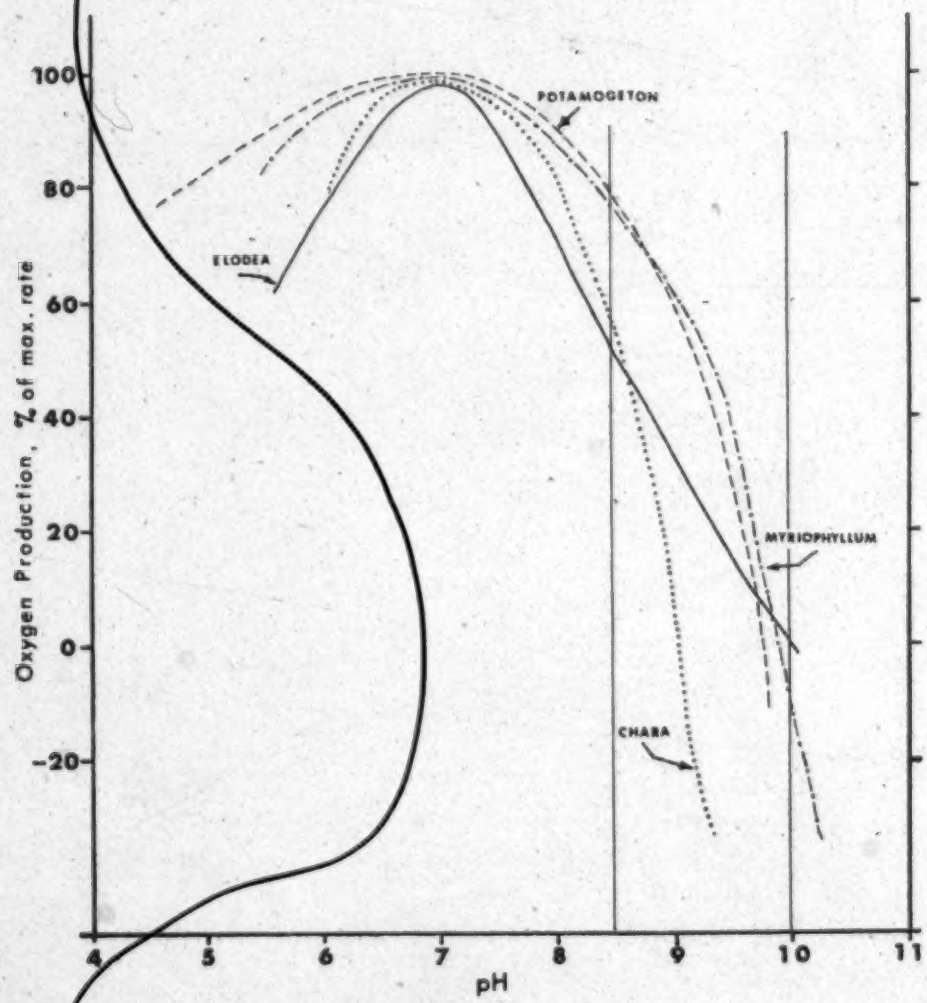

Oxygen Production, % of max. rate
100
80
60
40
20
0
-20
4
5
6
7
8
9
10
11
pH
POTAMOGETON
ELODEA
MYRIOPHYLLUM
CHARA

Fig. 16

The experiments produced two types of curves. The experiment with the *Myriophyllum* gave S-shaped curves which can be explained on the basis of carbon uptake either as free carbon dioxide or as bicarbonate. At pHs less than 5.5, free carbon dioxide is the dominant species so the rate of assimilation seen at these pHs is governed by its uptake and the light intensity. At pHs over 8, bicarbonate is the dominant species and the rate of assimilation is governed by the uptake of this ion and the light intensity. At pHs between 5 and 8, both species are present in varying proportions (Appendix III) and intermediate rates of assimilation are obtained. At very high pHs (over 10) net assimilation drops rapidly. At high pH the amount of carbonate in the solution becomes quite large and as carbonate is unuseable, the carbon supply diminishes. However, even at a pH of 11 there is still a large enough proportion of bicarbonate in solution if the total concentration is high, to enable assimilation to proceed at the maximum bicarbonate rate. The decrease in net assimilation that does occur at pHs over 10 would appear to agree with Steeman Nielsen's theory that it is the presence of hydroxyl ions which inhibits assimilation.

The curves generated by the first series of experiments show one maxima at pH 7 with no indication of a bicarbonate utilization "plateau" as seen in Fig. 17.

The pH may be shifted back and forth over a wide range with good reproducibility of the pH response curve. It appears that under the conditions used in these experiments a process other than the utilization rates of free carbon dioxide and bicarbonate is influencing rates of net assimilation.

FIGURE 17. Effects of pH on rates of net assimilation of *Myriophyllum exalbescens* under conditions of low and high concentrations of bicarbonate (50 and 100ppm bicarbonate at pH 8.3) under low and high light intensities (25 and 260 $\mu E/m^2/sec$)

(a) Data expressed as percentage of the maximum rate attained

(b) Data expressed in mg oxygen per hour per gm of organic matter.

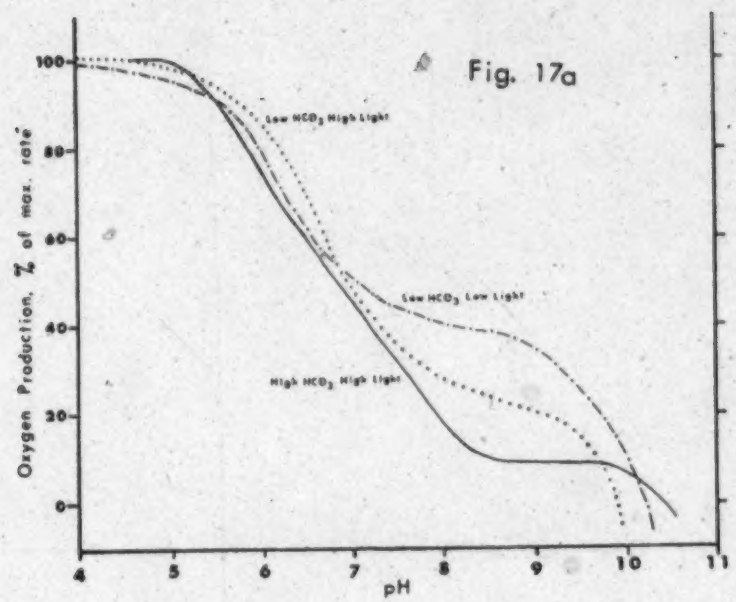


Fig. 17a

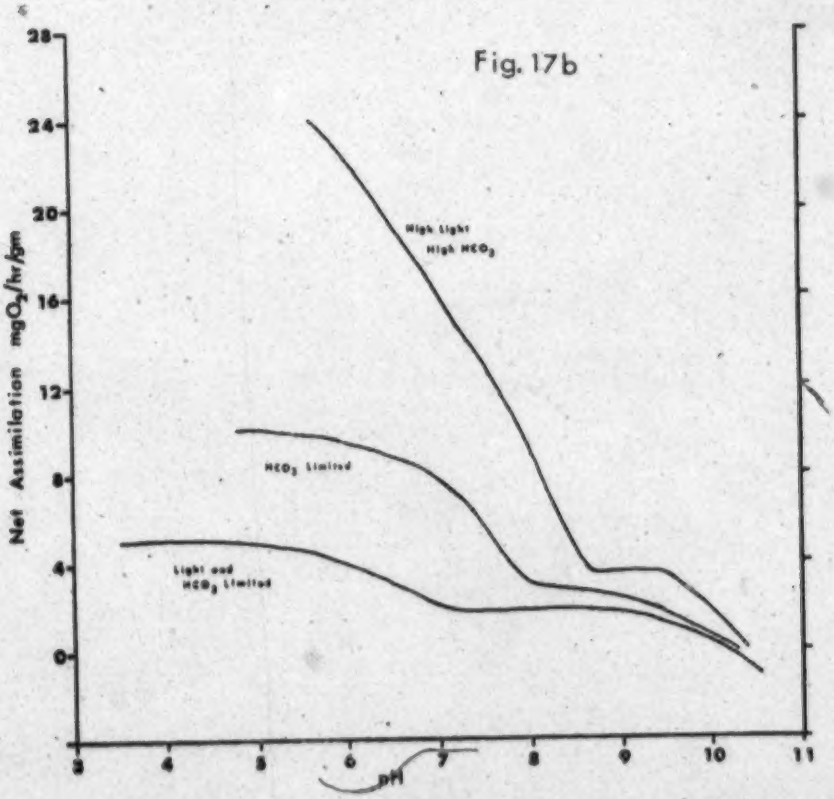


Fig. 17b

Reactions to Conditions of Anoxia

The four species were exposed to low oxygen concentrations by keeping them in the cuvette over night in complete darkness at 20°C. During this time they lowered the oxygen content of the water in the cuvette to values approaching zero. After about 18 hours in the dark the lights were turned on. *Elodea*, *Myriophyllum* and *Potamogeton pectinatus* began to produce oxygen after only a short lag period. *Chara* usually did not respond at all or did so at a greatly reduced rate. Exposures to conditions of anoxia for a period of four or five hours proved to be detrimental to *Chara*.

DISCUSSION AND CONCLUSIONS

Effects of Light and Temperature

Expressed on an organic weight basis, *Elodea canadensis* has the most efficient net assimilation of the four species studied under all light and temperature conditions used. Its maximum net assimilation rate was about 30 mg O_2/hr/gm at 25°C at pH 8.1. *Elodea* is particularly efficient at low light levels and its net assimilation rises very rapidly with increasing light intensities.

Myriophyllum exalbescens is the species which most nearly approaches *Elodea* in net assimilation rate. Its net assimilation rates were quite similar to those of *Elodea* under light-saturating conditions but under low light levels, *Myriophyllum* was not as active, especially at 15° and 25°.

Potamogeton pectinatus is efficient at low light levels where it approaches the rates achieved by *Elodea*. However, under high light intensities its saturation rates of net assimilation are well below those of *Elodea* and *Myriophyllum* at all three temperatures.

Chara has a very low rate of net assimilation - only about 20 to 30% of the rate of *Elodea*. It is not as efficient at low light levels as the other species and becomes light saturated at quite low intensities.

The respiration rates of the four species at three temperatures are shown in Fig. 15. The R_1 values obtained after the plants had been in the dark for a time are those rates which would most nearly approximate night-time respiration rates. The R_2 values obtained immediately after intense illumination are assumed to be the steady respiration rates occurring during photosynthesis when saturating

oxygen concentrations occur inside the cells. The large differences between R_1 and R_2 could indicate that there is some photorespiration occurring. However it is probable that, to a great extent, the higher respiration rates measured after illumination are produced by the saturating concentrations of oxygen that are present in and around the cells.

In general, the respiration rates of the four species follow the same rank order as their net assimilation rates. *Myriophyllum*, however, has a net assimilation rate similar to that of *Elodea* under high light conditions, but its night-time respiration rate is significantly higher.

Aquatic plants growing at depths where the light levels are low operate in a region where both light and temperature levels are critical. Plants can survive at a given depth only when the day-time net assimilation exceeds the night's respiratory losses by some acceptable margin. If the plants are subjected to conditions which produce defecits for any substantial lengths of time they will consume their reserves and eventually die.

Deficit conditions can be produced by lowering the light levels. This may occur with high turbidity, cloudy weather, ice cover or by mutual and self shading. The amount of detritus, epiphytes and marl accumulating on the plants may act to significantly reduce the amount of light reaching the photosynthetic tissues. *Chara* grows close to the bottom and in deeper water the *Chara* itself tends to produce a current-free zone near it. This enables detritus to collect on the plants. *Chara* is also noted for its production of marl which may reach a considerable thickness late in the season. In contrast,

Elodea and *P. pectinatus* are more flexible and grow well above the bottom into water which is circulating so that detritus does not collect on the leaves as easily. Marl may accumulate on their leaves but, because of their flexibility, the marl easily flakes off if the plants are disturbed. *Myriophyllum*, particularly as it ages, serves as a substrate for many organisms to live on and these also tend to lower net assimilation.

If light level and its duration are not limiting, an increase in temperature would be beneficial to the plants causing more rapid growth. If the plant is living at a subsistance level with respect to light, an increase in temperature will produce an increase in the respiration rate which could cause the plant to go into a deficit condition. *Chara* in particular, with its low rate of net assimilation, is susceptible to damage at low light levels. Its reserves of carbohydrates are low when compared to the other species and so cannot tolerate a deficit condition for a prolonged period of time.

Effects of pH

The pH experiments showed that the net assimilation of all the aquatic macrophytes studied is strongly affected by pH, especially at low light levels where the carbon supply is not limiting. *Myriophyllum* and *P. pectinatus* are normally found in moderate to very alkaline waters in Alberta. At pHs of 8.5 to 10, which represents the range of most lakes in central Alberta, these two plants are able to carry out net assimilation at rates which are close to their respective maxima. *Chara*, especially, and *Elodea* perform poorly at high pH values. *Elodea* has been found growing at high pH but the plants were located only in the shallow water. *Elodea* has not been found in a sufficient

number of lakes and streams in Alberta to clearly define its preferred conditions for growth. *Chara* has not been found in our survey of lakes in any body of water where the pH was above 9 or where blue-green algal blooms regularly occurred. Although the light levels in a lake during an algal bloom may be severely reduced, the pH produced by the algae would be enough to inhibit net assimilation by *Chara*.

Effects of anoxia.

Chara's susceptibility to anoxic conditions make it particularly vulnerable to starvation and death. The sediments in most lakes of central Alberta are anaerobic and *Chara*, growing in still water near these sediments, can easily suffer from oxygen deprivation. This is especially so when large amounts of organic material from algal blooms or from other macrophytes fall to the bottom and decay. *Chara*'s preference for a sandy bottom and shallow water is probably a consequence of this aspect of its physiology.

GENERAL DISCUSSION

The most significant effect of the heated effluent from the power stations is to prevent the formation of ice over large areas of the lake and to reduce the thickness of the ice and snow cover around them. This in turn increases light intensity in the water column to a level where macrophyte growth can occur. *Elodea* is able to grow under these conditions whereas other species are dormant. In this way *Elodea* gets a head start each spring and is able to crowd out and shade the other species.

Elodea is also successful in spreading in the lake because of its ability to form large numbers of vegetative propagules throughout most of the year. Those produced in the fall are able to become established with little competition when the other species are in a senescent condition and forming overwintering structures. A steady supply of propagules from the heated areas has contributed to the rapid and successful colonization of areas which are less affected by the thermal discharges from the power stations.

The studies of net assimilation in relation to light and temperature in the pH range of 8.0 to 8.5 typically encountered in Lake Wabamun, showed that *Elodea* had a significantly higher net assimilation than the other three species examined under all experimental conditions. It is able to assimilate better during cloudy weather or at depths where the other species are at or below compensation. It is likewise able to assimilate better than the other species at the higher temperatures prevailing near the mouths of the discharge canals. *Chara*'s low rate of net assimilation coupled with a relatively high rate of respiration do not enable it to survive at even moderate depths if subjected to

thermal discharge.

It has been noted (Allen and Gorham, 1973) that above-normal hours of sunshine together with below-normal water levels lead to heavy macrophyte growth. The amount of sunshine in May and June plays a particularly important role in determining growth for the season. Water level variations which occur in the lake are probably not as important in influencing growth as the hours of bright sunshine. Based on the measured diffuse attenuation coefficient of 0.7, a 30cm variation in water level will change the intensity of the light reaching the plants by 19%. Since the plants become light saturated at 5 to 10% of full sunlight, a variation of 20% brought about by water level fluctuations will not affect assimilation as much as a 20% variation in monthly hours of bright sunshine which may be expected in the Edmonton area.

Thermal discharges into Lake Wabamun have changed the environmental conditions of the lake sufficiently to favour the establishment and rank growth of *Elodea*. This plant, because of its characteristic growth habits, has become an obnoxious weed in the lake. The only effective long-term solution to the problem would be to completely stop the addition of heat to the lake by the power stations. It is not possible as yet to predict precisely what effects this will have on the growth and phenology of *Elodea*. A complete return of the ice cover would be necessary to gain the greatest benefits and this will require that there be no circulation of water into the lake from the power stations. *Elodea* has become so well established over large areas of the eastern end of the lake that it is extremely doubtful that the species would completely disappear from the areas it has colonized if the addition of heat were stopped. *Elodea* would lose

much of its competitive advantage and the density of the beds would probably decrease allowing the original species to make a comeback. This process may take several years to complete. Like many neighboring lakes the eastern end of Lake Wabamun was densely populated by submerged macrophytes before the power stations were built, and the removal of the heated effluents from the lake will not cause it to become weed-free.

Elodea has not been as successful in other lakes which have ice cover because its phenology is more similar to the endemic, well-established species and it must compete with them on a more even, if not inferior basis. *Elodea's* lowered rate of net assimilation at high pH may also prevent it from spreading in these other lakes. Most of the lakes in central Alberta have high pHs-especially while they are producing blooms of blue-green algae. The rate of net assimilation of *Elodea* at pH 9.5 is only 20% of the rate of its pH optimum, while the net assimilation of widely distributed species like *Myriophyllum* and *P. pectinatus* at pH 9.5 is 60% of their optima. The similar effect of high pH on net assimilation of *Chara* probably accounts for its limited distribution since it has not been found in any of the lakes surveyed in which the pH was above 9 or where algal blooms occur regularly.

In this study the effects of light intensity upon the growth of submerged macrophytes were of principal concern. Little or no attention was paid to effects of light quality other than to establish that with increasing depth in the lake there is selective attenuation of the red and blue ends of the spectrum. Growth at depth normally takes place, therefore, in yellow-green light of comparatively low intensity. As

the plants elongate towards the top of the water column the light quality as well as the intensity change until they reach full sunlight at the surface. There, it was noted, some species undergo pigment changes and/or bleaching. From what is known about the effects of light quality on the physiology of terrestrial plants, it is reasonable to suppose that different species of aquatic macrophytes may have developed a number of significant physiological responses to light quality and intensity gradients affecting such processes as photosynthesis, dormancy, flowering and morphogenesis. Further detailed field and laboratory studies of these possibilities are obviously needed and are likely to prove very rewarding.

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APPENDIX I

List of Lakes and Rivers Examined for Submerged Macrophytes.

Antler
Beaverhill
Bonny
Cache
Carson
Cooking
Danard
Disney
East Twin
Garner
Hanmore
Isle
La Nonne
Lessard
Mann (Upper and Lower)
Matchayaw (Devil's)
Micquelon
Pigeon
Redwater River
Sandy
Siebert
Smokey
Spring (Edmonton Beach)
Ste. Anne
Sturgeon River (at Gibbons)
Thunder
Vincent
Wabamun
Wizard

APPENDIX II

Locations where *Elodea* sp. has been found in Alberta.

Location	Date	Collector
North edge of Milk River Ridge	July 20, 1885	J. Macoun
NW of Calgary in a ditch	July 30, 1953	W.C. McCalla
Near Gem, N. of Brooks	August 20, 1954	E.H. Moss
Near Vauxhall	September 4, 1955	E.H. Moss
Sturgeon River near Onoway	August 18, 1958	G. Pegg
Wabamun Lake	May 14, 1970	E.D. Allen
Isle Lake	June 29, 1971	E.D. Allen
Danard Lake	August 2, 1971	E.D. Allen
Matchayaw (Devil's)	August 2, 1971	E.D. Allen
Sturgeon River (Gibbons)	September 1, 1971	P.R. Gorham

[1] Voucher specimens for all collections except that of J. Macoun are deposited in the Herbarium, Department of Botany, University of Alberta. The Macoun collection is deposited in the National Herbarium, National Museum of Natural Sciences, Ottawa, Canada.

APPENDIX III

Relationship between free carbon dioxide, bicarbonate and carbonate with pH.

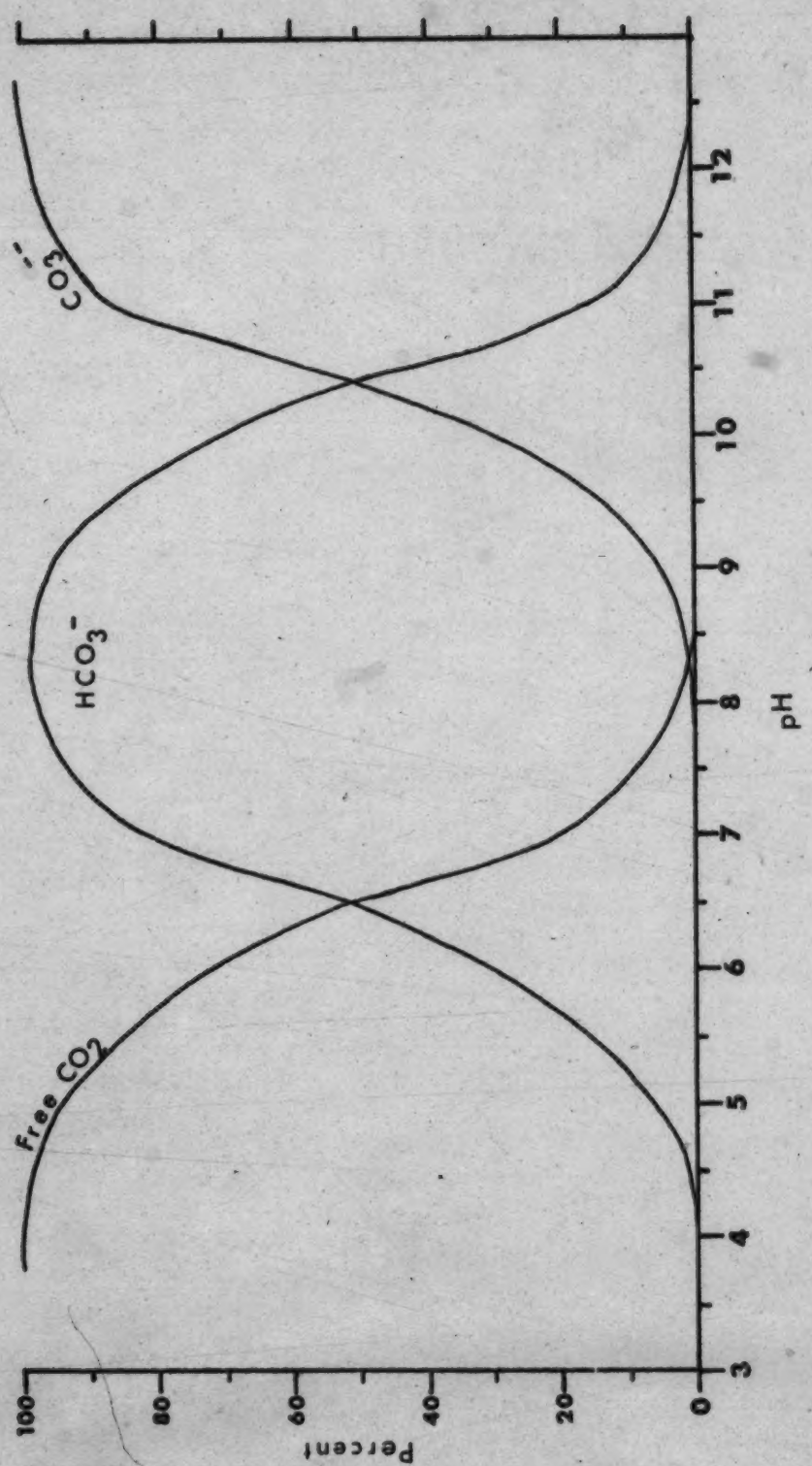
The proportion of free carbon dioxide and carbonate present in a solution with a given pH on the accompanying two graphs is calculated from the following equations. The amount of bicarbonate in the solution is determined by subtracting $\%CO_2 + \%CO_3^{--}$ from 100%.

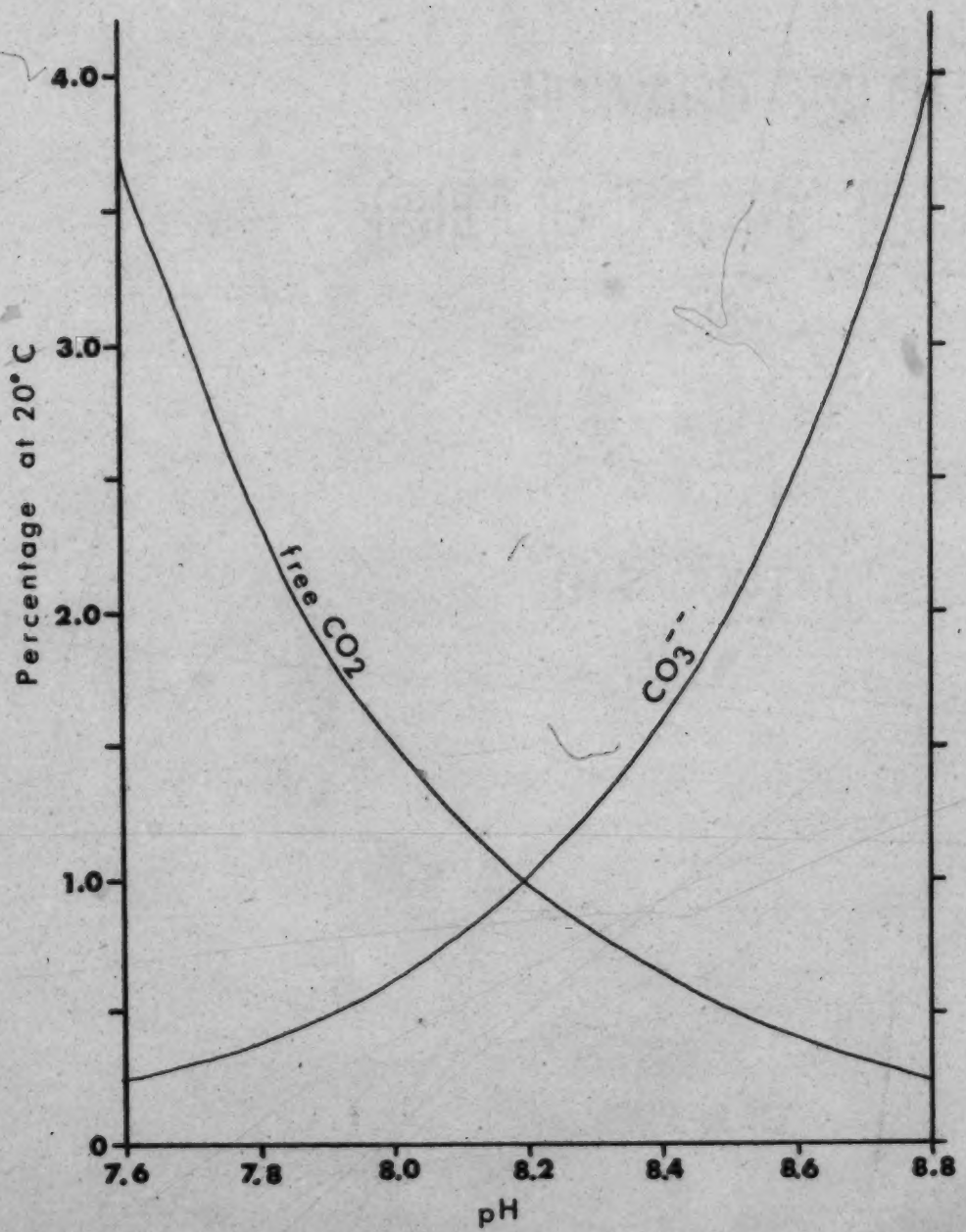
$$\%CO_2 = \left(\frac{1}{1 + \frac{K_1}{10^{-pH}}} \right) \times 100$$

$$\%CO_3^{--} = \left(\frac{1}{1 + \frac{10^{-pH}}{K_2}} \right) \times 100$$

where $K_1 = 4.17 \times 10^{-7}$ at $20^{\circ}C$

$K_2 = 4.17 \times 10^{-11}$ at $20^{\circ}C$


Free CO_2
HCO_3^-
CO_3^{--}
Percent
pH
100
80
60
40
20
0
3
4
5
6
7
8
9
10
11
12


4.0
3.0
2.0
1.0
0
Percentage at 20° C
free CO2
CO3--
7.6
7.8
8.0
8.2
8.4
8.6
8.8
pH